# The decline of Steller sea lions (*Eumetopias jubatus*) in the North Pacific: insights from indigenous people, ethnohistoric records and archaeological data

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# Abstract

A number of hypotheses have been proposed to explain the most recent decline (1977–2012) of Steller sea lions (SSL; Eumetopias jubatus) in the Gulf of Alaska and Aleutian Islands. We examined hypotheses about fisheries competition, environmental change, predation, anthropogenic effects and disease using observations of modern Aleut and archaeological, ethnohistoric and ethnographic data from the western Gulf of Alaska and Aleutian Islands. These data indicate that Steller sea lion numbers have declined and recovered repeatedly over the past 4500 years and were last at critically low numbers during the 1870s-1930s. Steller sea lions appear to have been more abundant during the cool periods – and lower during the warmer periods. Observations by local peoples, explorers, early government surveyors and biologists since the late 1800s suggest that low populations of SSL have been associated with high populations of Gadidae fishes (Pacific cod - Gadus macrocephalus and walleye pollock - Theragra chalcogramma) and are consistent with the ocean climate hypothesis to explain the decline of sea lions. They suggest that removals by people and killer whales (Orcinus orca) did not cause the sea lion declines, but could have compounded the magnitude of the decline as sea lion numbers approached low densities. Archaeological, anthropological and ethnohistorical analvses demonstrate that fluctuations have occurred in the North Pacific over hundreds to thousands of years and provide context for understanding the changes that occur today and the changes that will continue to occur in the future.

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Received 30 Apr 2012 Accepted 6 Mar 2013

**Keywords** Aleut, archaeology, killer whales, ocean climate, regime shifts, Steller sea lion, traditional knowledge

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# Introduction

Between 1977 and 1988, Steller sea lions (SSL; *Eumetopias jubatus*) in the Gulf of Alaska and Aleutian Islands declined from a high of nearly 250 000 individuals to <100 000 (Trites and Larkin 1996; NRC 2003). The decline proceeded at a slower rate through the 1990s and levelled off with fewer than 40 000 sea lions remaining at the turn of the century (Fritz and Brown 2005). However, the western population of SSL has continued to decline in the western and central Aleutian Islands (NMFS 2010).

Research conducted to date into the decline of the western population of SSL has provided a better understanding of the life history of sea lions and the factors that might have contributed to their decline (DeMaster and Atkinson 2002; NRC 2003). But there is of yet no consensus about the proximate and ultimate causes of the declines, and resource managers have taken precautionary measures prohibiting commercial groundfish harvesting in many areas of the Gulf of Alaska and Bering Sea, particularly around sea lion rookeries and haulouts (Fig. 1; NRC 2003; NMFS 2010; Durban 2010; Bernard et al. 2011; McBeath 2012). Hypotheses to explain the declines range from a reduction in food sources caused by commercial harvesting of groundfish, to disease, predation by killer whales (Orcinus orca), contaminants, illegal shooting and ocean climate change (Alverson 1992; DeMaster and Atkinson 2002; NRC 2003; Trites and Donnelly 2003; Trites et al. 2007b.c).

Scientific knowledge about sea lions dates back only 55 years to the first population census in 1956 (Mathisen and Lopp 1963). These and subsequent counts and surveys made in the 1960s and 1970s (Trites and Larkin 1996) have become the benchmark for what is commonly considered to be pristine numbers of sea lions – the numbers that would be present in the absence of the commercial fisheries or harvests of the last 40 years. However, the oral histories told by Aleut native people of the Aleutian Islands and Gulf of Alaska and the archaeological data from the villages of their ancestors suggest that this short-term assumption about pristine numbers may be erroneous.

Aleuts are one of the least known or studied northern peoples. They have occupied the Pribilof Islands for the past 200 years and have lived on the eastern Aleutian Islands, Alaska Peninsula and the Shumagin Islands for more than 10 000 years. They have a long oral history and an archaeological record left by their ancestors of sea lion harvesting that provide a historical context for understanding the causes of the sea lion decline. These archaeological data provide a longer-term record of the relative interactions that people have had with the marine environment spanning hundreds to thousands of years. Modern-day Aleut hunters and fishermen also have insights to provide as they continue to acquire detailed ecological knowledge of the coastline, currents, weather and the frequency and behaviour of marine species that inhabit the region. The role of local peoples in collecting population data for conservation and ecological studies has a long history and has gained prominence (Freeman 1992; Colchester 1994; Brush and Stabinsky 1996; Berkes 1999; Ortiz 1999; Weber et al. 2000; Sheil and Lawrence 2004; Brook and McLachlan 2008).

Archaeological data can reveal long-term trends in the distribution of SSL over 4500 to ca.



**Figure 1** Greater Aleutian region and Alaska Peninsula showing Steller sea lion breeding (rookeries) and resting (haulouts) sites, as well as study sites and locations referred to in the text.

250 years before present, while ethnohistory, ethnography and traditional knowledge can uncover medium-scale trends over the last 200 years. We use these data to evaluate six of the seven initial hypotheses that have been proposed to explain the decline of SSL: (i) fisheries (ii) competition, (iii) environmental change, (iv) predation, (v) anthropogenic effects and (vi) disease. We considered the interactions between factors, but had no data to evaluate (vii) contaminants. We also compiled information about historic population trends of sea lions extending hundreds to thousands of years into the past. As shown in the following, the suite of general commentary obtained from the modernday Aleut peoples provides a rich body of qualitative assessments and observations that, when combined with the ethnohistoric and the quantitative archaeological data, provide important contributions to the major hypotheses that have been proposed to explain the decline of the Steller sea lion in the Gulf of Alaska and Aleutian Islands.

#### Materials and methods

# Study areas and data sources

The ancient Aleut and many of their North Pacific neighbours were unlike most foraging peoples elsewhere in the world because they lived in large, permanent towns, had strong institutions of rank and status, owned slaves and participated in long-distance military campaigns (Townsend 1983; Black 1984; Veniaminov 1984; Maschner and Reedy-Maschner 1998). Accordingly, the Aleut used marine resources such as Gadidae (Pacific cod -Gadus macrocephalus and walleye pollock – Theragra chalcogramma), salmon (Oncorhynchus sp.) and sea mammals not just for subsistence, but as commodities that were traded for status and prestige, power, rare goods and other social, political and material products (Lantis 1970, 1984; Maschner and Hoffman 2003; Orchard 2003; Reedy-Maschner and Maschner 2004). With the arrival of the Russian fur traders and later with the American government, various aspects of this economic system changed in emphasis, but never altered its basic form (Reedy-Maschner 2010). Today, the approximately 3000 surviving Aleut represent a small but vibrant portion of the 20 000–30 000 people who lived in the region prior to European diseases and conflict (Lantis 1970, 1984). They still participate in an economic system focussed on the use of the marine ecosystem.

In the past, Aleuts hunted sea lions to obtain meat, oil and blubber for eating, bones and whiskers for tools and other needs, sinew for cordage, intestines and stomachs for waterproof containers and clothing, and most importantly, skin for baidarkas (kayaks; Laughlin 1980; Veniaminov 1984). Until recently, annual subsistence harvests of sea lions occurred in most coastal communities in the geographical range of the species (Wolfe and Mishler 1993). In 1992, 2 years after the Steller sea lion was designated as a threatened species, numbers of SSL taken for subsistence purposes dropped dramatically under the mistaken impression that subsistence harvests were banned (Wolfe and Mishler 1993), an impression still common 20 years later. Today, sea lions are most often harvested in the western Aleutian and Pribilof Islands and are occasionally hunted by eastern Aleutian Island communities. They are rarely hunted by communities of the Alaska Peninsula region, but are still observed closely by local residents and fishermen.

#### Oral history, ethnography and ethnohistory

Oral historic and ethnographic data were obtained from 52 interviews conducted with young and old fishermen in the western Gulf and southern Bering Sea communities of King Cove, Sand Point, False Pass, Akutan and Nelson Lagoon following methods developed by Reedy-Maschner (Reedy-Maschner 2004. 2010: Reedv-Maschner and Maschner 2004). These were unstructured interviews that allowed the participants to express ideas, observations and knowledge over a range of topics. We documented traditional ecological knowledge related to SSL in King Cove and Sand Point during the salmon, cod, halibut and crab fishing seasons, and in Nelson Lagoon, False Pass and Akutan in the off seasons. The focus of these interviews was on their observations of SSL throughout their lives, subsistence hunting and use in previous years, and data on predators and prey.

We analysed the interviews and identified common themes and events. Common descriptions of events were cross-checked using Reedy-Maschner's genealogy of the region (over 4000 individuals) to distinguish between first-hand observations and stories that were passed along kinship lines. While not directly quantifiable, the results of such analyses tend to be more useful than blind surveys because every observation made by an individual can be cross-checked with the observations made by others and can be assessed for accuracy using comparative data.

We supplemented our interview data with a number of subsistence surveys and ethnographic interviews recently conducted by Reedy-Maschner in Akutan, False Pass and Nelson Lagoon as part of a project to identify current subsistence trends and the potential impacts of development in this region. In total, data relating to human interactions with SSL were collected on over 100 households in the western Gulf of Alaska and southern Bering Sea.

In addition to conducting interviews, we systematically surveyed and analysed ethnohistoric sources that ranged from observations by eighteenth and nineteenth century explorers, traders, missionaries and naturalists (e.g. Choris 1822; Veniaminov 1984), to the observations of early US surveyors, fisheries managers and other bureaucrats (e.g. Elliot 1882; U.S. Census 1890). Data pertaining to the long-term history of SSL in the region, and observations of potential causes for variations in their distributions, were catalogued and recorded. In addition, we reviewed and systematically analysed the extant ethnographic sources for data pertinent to our study (e.g. Black 1981; Jochelson 2002).

# Archaeology

We compiled archaeological data about SSL from over 12 seasons of field research from the Lower Alaska Peninsula Project and the Sanak Island Project in the western Gulf of Alaska and southern Bering Sea. These data consist of hundreds of thousands of marine mammal, bird and fish bones from over 300 ancient village sites spanning the last 6000 years and represent the largest zooarchaeological data sets in the southern Bering Sea and North Pacific region (H.D.G. Maschner, unpublished data). Marine mammals recovered include SSL, northern fur seals (NFS; *Callorhinus ursinus*), sea otters (*Enhydra lutris*), bearded seals (*Erignathus barbatus*), ringed seals (*Pusa hispida*), harbour seals (*Phoca vitulina*), spotted seals (*Phoca largha*), Pacific walrus (*Odobenus rosmarus*) and a number of species of Cetacea. We identified faunal elements to the lowest taxa possible (species), but identified some body parts, such as phalanges, ribs and vertebrae only by family or more general categories (i.e. phocidae – primarily harbour seals and spotted seals, or otariidae – sea lions or fur seals).

The archaeological record of Steller sea lion harvesting provides a means to track long-term interactions between humans, SSL and changing environmental conditions. The high-resolution data we present were derived from 35 dated archaeological components (distinct deposits) from 27 village sites on the western Alaska Peninsula, Unimak Island and the Sanak Archipelago (Fig. 1). Each component was a stratigraphically and temporally distinct layer in an archaeological site. The deposits at the village sites ranged in age from ca. 4500 to 250 years before present. Associated radiocarbon dates of collected materials were derived from charcoal and calibrated using Calib 6.0 (CHRONO Centre, Queens University Belfast, Belfast, Northern Ireland) to adjust for calendar years before present (Table 1).

We assessed trends in the distributions of SSL and other species in two ways. First, we calculated the contribution of SSL, NFS, phocids and sea otters to Aleut subsistence over the last 4500 years as percentages of the number of identified specimens (NISP) of mammal bone in the archaeological collection. Second, we calculated an index of abundance (AI) representing a normed ratio of the NISPs of a high-ranked taxa (A) to the NISPs of a lower-ranked taxa (B), measured as AI = A/(A + B) (e.g. Bayham 1979; Ugan and Bright 2001) where rank is measured by body size, a good proxy for overall caloric return. Values close to 0 indicate a complete absence of the highranked taxon (A), while values close to 1 indicate a dominating presence.

The index of abundance incorporates an assessment of caloric rank, which means that declines in AI can be interpreted as a decrease in overall foraging efficiency and therefore encounter rates of the high-ranked taxa (Lyman 2003; Ugan *et al.* 2003). Such declines are believed to reflect a form of resource depression of the high-ranked taxon [for in-depth discussion of this relationship and the calculation of these indices see Betts and Friesen (2006) and Lyman (2003)]. These indices of abundance are therefore useful for assessing human and natural impacts on animal abundances because they can be linked to the prey choice model (e.g. Charnov 1973; Stephens and Krebs 1986) in a manner that typical NISP calculations cannot.

We calculated AIs for NFS, SSL and otariids (NFS and SSL combined) using both sea otters and phocids (primarily harbour seals and spotted seals) as the lower-ranked taxa. For comparative purposes, we also calculated AIs for sea otters using phocids as the lower-ranked taxon. Calculating multiple indices controls for possible perturbations in the abundance of the low-ranked or 'B' taxon reducing the possibility of misattributing a resource depression where none has occurred (Betts and Friesen 2006).

As proxy measures of Steller sea lion abundance, we used two other categories of data. First, we analysed data on hundreds of North Pacific spear points and end-blades spanning the last 5500 years. Spear point length is a proxy measure of access to shore-bound large mammals because large, thrusting spears are used when large sea mammals can be taken on the beach, and smaller end-blades and toggling harpoons are a measure of offshore sea mammal hunting. During periods of increased productivity and thus expansion of large sea mammal populations, there should be an increase in the numbers of large thrusting spears and a decrease in this category during periods of low numbers of large sea mammals. These changes should also be reflected in d15N stable isotope values of human remains. Using data presented by Coltrain et al. (2006), we analysed d15N as a measure of the contribution of high trophic feeding prey to the Aleut diet for 80 human skeletons recovered from the Umnak Island area with dates spanning the last 3600 years.

We compared the abundance of SSL (as measured by AI) and the other proxy data with climatic conditions spanning 4500 years (Table 2). Measures of climate were based on pollen cores, other data of the Alaska Peninsula Project (Jordan and Maschner 2000; Jordan and Krumhardt 2003), regional proxy data (Mann *et al.* 1998, 2002; Anderson *et al.* 2001, 2005; Hu *et al.* 2001) and studies of the Pacific Decadal Oscillation (Mantua *et al.* 1997; Biondi *et al.* 2001). The measures of climate generally reflect changes in air temperatures which correlate with sea surface

Table 1	Mammal f	aunal elen	nents (n =	20 845)	identified fr	om 35 dat	ed archae	ological co	omponents	s in 27 vil	lage si	tes.					
Site	Date BP	Misc. pinniped	Misc. otariidae	Steller sea lion	Northern fur seal	Misc. phocidae	Harbour seal	Ringed seal	Bearded seal	Spotted seal	Sea otter	Caribou	Porpoise	Large cetacean	Total Number of Individual Specimens (NISP)	Total phocidae	Total otariidae
XFP-050	180	12	23	12	4	67	7	0	0	0	18	0	-	2	146	74	39
UNI-067	350	162	287	138	4	101	12	0	0	0	ო	16	0	ო	728	113	429
XFP-052	350	69	44	42	9	102	0	0	0	0	78	-	0	13	355	102	92
XFP-099	382	9	18	25	6	37	ო	0	2	0	8	2	0	0	110	42	52
XFP-104	388	0	26	5	-	191	0	0	0	0	ო	0	0	0	228	191	32
XFP-121	403	20	=	-	-	38	0	0	0	0	12	-	0	-	87	40	13
XFP-133	423	9	ო	0	10	28	-	0	0	0	24	-	-	15	91	29	15
XFP-110	443	14	11	13	0	40	ო	0	0	0	32	0	0	16	131	43	26
XCB003	560	5	25	9	ო	62	9	5	0	-	9	0	0	0	121	74	34
XCB028	565	9	5	4	9	19	33	0	0	0	0	17	0	0	92	52	15
XFP-119	602	4	7	2	0	13	0	0	0	0	32	0	0	11	69	13	6
UNI071	640	0	0	10	4	0	4	0	0	0	38	32	0	0	88	4	14
XFP-056	920	49	48	6	9	275	Ð	0	0	0	169	-	0	26	588	280	63
Lower:B																	
XFP-056	1400	137	24	Ð	5	91	-	0	0	0	71	0	0	13	347	92	34
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XFP-038	1796	ຕ ເ	N I		6 0	29	0	0 1	0 1	0 1	17	- ;	0 0	4 0	72	29	18
XCB1058	2000	17	271	35	DE I	16/	1/3	66 202	ں م	۵ <u>,</u>	16	14	0 0	0 0	1323	1029	23/
XCB1059	2000	0 0	591 	100	11	3483	345	306 î	9	12	88 10	82,	0 0	0	5090	4152	768
XFP-058	2040	168 î	/8	10	19		4 (	э,	0 0	0 0	922	- 0	N	01	688	c/ ۱ ح	10/
XFP-119B VED.064	2040	5 0	05 0 t	97 70	24	0/		- 0	<b>)</b> (	5 0	102	5 0	5 0		358	1/	02 02 02
VED ODE	1000	5		~ Ŧ	<u> </u>	107	- c		1 0		200		۰ <del>،</del>	- 0	197		1 0
XFP-031	2184	116	22	- 19	1 10	35	0	0 0	v	0 0	8 8	0 0	- 0	47	279	2 88	46
XCB1051	2200	338	539	92	06	2524	274	205	23	5	112	64	0	0	4266	3031	721
XCB1053	2200	111	126	12	11	717	160	23	б	0	56	12	0	0	1237	606	149
XFP-063	2232	0	27	10	31	73	-	0	0	0	30	0	0	-	173	74	68
XFP-096	2249	72	40	4	4	75	0	0	0	0	92	0	0	6	298	77	48
XFP-036	2355	0	4	4	0	33	-	0	0	0	15	0	з	5	67	34	10
XFP-061	2567	115	42	12	4	661	14	-	0	0	163	0	-	14	1027	676	58
XCB105E	2570	24	24	2	0	200	36	13	<del>.</del>	<del>.</del>	-	62	0	0	364	251	26
XFP-067	2571	45	38	9	e	58	4	0	-	0	94	-	0	14	264	63	47
XFP-062	3300	2	12	ლ I	0 ·	35	<del>.</del> .	0	0	0	13	0	0	<del>ი</del> ი	74	36	15
XFP-063	3600	10	24	2	<del>.</del> - 1	21	<del>-</del> -	0	0	0	30	0	0	2	96	52	32
XFP-054	3750	46	16	ო	N	42	4	0	0	0	-	0	0	13	127	46	21
XFP-111	4507	42	13	9	0	382	4	0	0	0	630	0	0	21	1100	388	19

Period	Age range	Approximate climatic conditions
Recent era	100 BP-Present Day	Very warm
Little ice age	700–100 BP	Cold and wet
Medieval climatic anomaly	1100–700 BP	Warmer and dryer, variable
Pre-medieval climatic anomaly	1800–1100 BP	Colder?
Roman warm interval	2100-1800 BP	Warmer
Neoglacial	2600–2000 BP	Cool and wet (increased storminess)
	3000–2600 BP	Perhaps warmer
	4000–3000 BP	Cool and wet
Altithermal	5200-4000 BP	Warmer
	5600-5200 BP	Cooler
	6200–5600 BP	Warm and wet
	9000-6200 BP	Dry and variable with warmer intervals

Table 2 Climatic regime shifts in the western Gulf of Alaska and southern Bering Sea region.

Grey fill represents periods with significant changes in air temperature which correlates with sea surface temperatures, storminess, and ocean circulation, conditions that drive ocean productivity (Misarti *et al.* 2009). Data were reconstructed from various climatic proxies for the North Pacific, Gulf of Alaska, and greater Bering Sea region (Huesser *et al.* 1985; Mann and Hamilton 1995; Mason *et al.* 1995; Budd *et al.* 1998; Mann *et al.* 1998; Calkin *et al.* 2001; Hu *et al.* 2001; Mann 2001; Finney *et al.* 2002; Jordan and Krumhardt 2003; Magny and Haas 2004; D'Arrigo *et al.* 2005; Loso *et al.* 2006; Misarti 2007; Misarti *et al.* 2009, 2012). Adapted with modification from Maschner *et al.* (2009a).

temperatures, storminess and ocean circulation (Trites *et al.* 2007c).

As part of the broader research efforts in the region, we used a human occupation index (HOI) as a proxy measure to track human population trends in the region as described by Maschner *et al.* (2009a). We then compared the long-term trends in the distribution of SSL, as measured by the abundance indices, diet and technology, with the HOI, and with measures of human population based on archaeological settlement data and radio-carbon date frequencies (e.g. Munoz *et al.* 2010). Integrating such multiple scales of inquiry from the modern, to the historic, to the deep time of the palaeoecological record, allows the dynamic population histories of North Pacific sea mammals and their complex ecologies to be reconstructed.

# **Results and discussion**

#### Population trends: short term

Historical reductions have been noted for a number of marine species in Alaska (Table 3). All of the Aleuts that we interviewed who were over 50 years of age (n = 22, 44%) said that the current decline of sea lions was not the first time there have been major declines in the numbers of sea mammals in the region, and some of the oldest fishermen also mentioned directly that there were

periods in their father's or grandfather's times when sea lion populations were low, particularly before the 1940s (Table 4). Aleut oral histories and the ethnohistoric records describe significant previous declines of sea mammals in the 1870s, as well as periods of abundance, and fundamental changes in the ecology of the North Pacific over the last 200 years.

# Population trends: long term

The archaeological record of the Aleut use of marine species such as the Steller sea lion spans 10 000 years (Laughlin 1980), but well-preserved quantifiable samples are only found from the last 4600 years (Tews 2005; Maschner et al. 2008, 2009a; Betts et al. 2011). Yesner (1980, 1981) points out that the Aleutian region is one of the most productive and biologically diverse ecosystems in the northern hemisphere and that the peoples of the area were poised and equipped to harvest those resources (cf. Black 1987; Veltre 1998). As Yesner (1980) and others have discussed (Simenstad et al. 1978; Laughlin 1980; Yesner 1987, 1988; Siegel-Causey et al. 1991; Maschner 1998; Savinetsky et al. 2004), the remains of mammals, birds and fish found in North Pacific archaeological sites are not only a good measure of relative abundance at the time of harvesting but also provide a measure of change

Date	Observation	Location	Source
1770s–1830s	Earthquakes, volcanic eruptions and tsunamis contributed to the loss of some breeding grounds in the Aleutians	Unalaska, Sanak, Attu and the Shumagin Islands	Black (1981)
1780	Decline in sea otters occurred after earthquake activity in the northern Kurile Islands	Kurile Islands	Black (1981)
1790–1810	Cod disappear from Unalaska, large numbers of Steller sea lions (SSL) reported. Steller sea lions outnumbered fur seals on the Pribilof Islands	Aleutian and Pribilof Islands	Black (1981); Choris (1822)
1820s	Several hundred thousand sea lions reported on the Pribilof Islands. Steller sea lions found in large numbers throughout the Aleutian chain	Pribilof Islands	Elliot (1881)
1830	Only on St. George Island were sea lions in high numbers and could be hunted like a fur seal. As the Aleut used the cured skins for <i>baidarka</i> (kayak) covering and intestines for <i>kamleis</i> (outer garments), 1500 skin pieces and 12 000 fathoms of intestines were prepared annually on St. George alone in the early nineteenth century	St. George Island	Wrangell (1980)
1839	SSL were on 'almost all Pacific coasts and islands from latitude 61° (and even farther north, since they have been seen, though rarely, on Stuart Island, at latitude 63.5°) to undetermined southern latitudes'	Bering Sea and Aleutian Islands	Wrangell (1980)
1870–1877	SSL in rapid decline. Huge increase in cod populations. Massive influx of Scandinavian cod fishermen and boats from the Pacific Northwest. Predatory attacks on sea lions by Orca. Atka Mackerel 'drove the sea lions away'. Collapse of the Steller sea lion populations in the 1870s led to widespread subsistence problems throughout the region when the total Aleut harvest did not meet basic needs. It was so serious that the U.S. Government started importing sea lion skins from California so that kayak construction could continue and prevent widespread starvation	Western Gulf of Alaska, Aleutian and Pribilof Islands	Black (1981); U.S. Census (1890); Elliot (1881); Maschner and Reedy-Maschner unpublished data; Nelson (1887); Reedy-Maschner (2010); Veniaminov (1984)
1873–1874	Recounted statements by Aleuts that the Russians drove sea lions off St. George Island (one of the Pribilof Islands) so fur seals would colonize the island, noting that St. George had been primarily covered in sea lions with fewer fur seals. 8000–10 000 sea lions were observed breeding around the outer edge of the seal rookeries on St. Paul. St. Paul Islanders annually captured about 200 or 300 sea lions for skin, meat, intestines, fat and sinew, with perhaps 30–40 sea lions caged at a time in a flimsy makeshift corral. Sea lions had no commercial value (except in the local Aleutian region for kayak covers), although the Chinese procured sea lion whiskers as pickers for opium pipes	Pribilof Islands	Elliot (1881, 1882, 1886)
1909	The local Aleut on Attu Island in the western Aleutians reportedly had to stop making kayaks sometime before 1909 because there were no sea lion skins to cover them. The large ocean-going boats built by the Aleut were no longer constructed because of a lack of Steller sea lion skins. This resulted in serious adaptive problems for the Aleut as they were no longer able to move families between islands	Attu Island	Jochelson (2002)

**Table 3** Summaries of ethnohistoric, ethnographic and oral testimonies on variations in sea mammal populations and human responses over the last 240 years. Potential or documented regime shifts are in grey.

#### Table 3 (Continued).

Date	Observation	Location	Source
1912	'Sea mammals like the sea lion, sea bear, the fur seal and the varieties of the common seal and of the whale are now rare near the coasts or have disappeared altogether from some of the islands'	Aleutian Islands	Jochelson (1912)
1920	Wooden dories completely replace Aleut kayaks, effectively ending the hunt for SSL	Aleutian Islands	Jochelson (1912, 2002)
1920s–1940s	'Once abundant, this animal (the Steller sea lion) is now greatly reduced in numbers, and it has disappeared from many of its former haunts. It is still numerous on Bogoslof Island'	Aleutian Islands	Collins <i>et al.</i> (1945)
1942–1945	Pacific cod disappear. Last caught in King Cove 1942 and last caught in False Pass 1945. Increase in SSL. Navy target practice on rookeries such as Clubbing Rocks	Western Gulf of Alaska	Interviews
1950s–1960s	SSL reported everywhere. No cod caught by local fishermen	Western Gulf of Alaska	Interviews
1940s–1970s	D. Pearson grew up with sparse numbers of sea lions during the 1940s and recalled their numbers increasing through the 1950s, 1960s and early 1970s	Kodiak Archipelago	D. Pearson pers. Comm. Cited in Trites and Larkin (1996)
1960s–1970s	A number of patterns were evident from interviews of local residents. Comments included: 'During the 1960s and 1970s, sea lions were seen everywhere', 'great herds of them' and 'thousands'. Every offshore island appeared to be covered: 'It looked like they were moving like a kaleidoscope', according to one elder speaking of the islands around Sanak, Cherni and the Pavlov Islands. 'Sea lions were on all of the small islands; used to be packed'	Western Gulf of Alaska	Maschner and Reedy-Maschner interviews in King Cove, Akutan, False Pass and Sand Point
1975–1977	Documented regime shift. Cod and Pollock fisheries save local fishermen and communities. Atka Mackerel populations explode in western Aleutian Islands much like the 1870s. Sea lion populations go into decline, also like the 1870s	Aleutian Islands and Western Gulf of Alaska	Interviews; Reedy-Maschner (2010)
2000s	First reported orca pods in Bristol Bay, predatory pods near False Pass. Similar to events reported after the potential 1870s regime shift	Southern Bering Sea and Western Gulf of Alaska	Interviews

Potential or documented oceanic regime shifts are in grey.

in the ecosystem relative to modern distributions (e.g. Braje and Rick 2011).

Abundance indices such as we calculated are usually considered to be robust measures when taphonomic and collection biases are similar in all the assemblages being compared (e.g. Ugan and Bright 2001; although see cautions by Lyman 2003). Following Charnov *et al.* (1976), such declines have been interpreted in other ecosystems as evidence of a 'resource depression' of large-bodied taxa resulting from human predation, environmental change or prey behaviour (e.g. Hildebrandt and Jones 1992; Broughton 1994, 1997, 1999; Janetski 1997; Butler 2000; Cannon 2000; Grayson 2001; Lyman 2003; Betts and Friesen 2006). Simenstad *et al.* (1978), for example, used archaeological and modern data to argue that there was a direct relationship between the over-exploitation of sea otters by the Aleut and the expansion of sea urchin communities, which in turn reduced kelp forests – the primary food source of these invertebrates.

In general, we found that the trends in relative abundances of Steller sea lion, fur seal and phocid remains followed similar trajectories and were out of phase (the inverse) with those of sea otters (Fig. 2a–c). Both the NISP frequencies and abundance indices indicate that the abundance of SSL was low during the initial occupation of the region by Aleuts and that sea lion numbers rose dramatically during the next millennium. This increase in sea lions was followed by a sharp decrease in abundance between 3000 and 2500 years ago, rising 2200–2000 years ago, and falling again through 900 years ago (e.g. Fig. 2b, Steller sea lion to sea otter AI). Sea lion populations did not increase again until about 600 years ago. NFS appear to have followed the general trends of sea lions (Fig. 2c) although the fur seal increase ca. 500 years ago is more ambiguous than the increase in SSL.

In addition to determining the abundance indices of sea lions and fur seals separately, we calculated abundance indices of all otariids combined because some otariid bone elements such as vertebrae, ribs and some phalanges were difficult to identify to species. These indices show that Steller sea lion, fur seals and the combined category of otariidae all followed a similar trajectory (Fig. 2b,c), while sea otters followed an opposite trajectory (Fig. 2a). We considered the possibility that the number of Steller sea lion elements in an assemblage was related to the distance of a village site from the nearest sea lion haulout or rookery because most Steller sea lion hunting was done at those locations. However, we found no relationship ( $r^2 = 0.0003$ ) between distance to the nearest modern haul-out or rookery and percentage of SSL (as a ratio of all seals and sea lions in the assemblage), although prehistoric populations may have been much more broadly distributed.

There are few indications from the associated artefact assemblages to indicate that shifts in abundances of SSL noted from the archaeological

Table 4         Summaries of oral testimonies on human – sea lion interaction and potential causes for the de	cline.
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Location	Торіс	Observation	Source
Sand Point, King Cove, False Pass	Interactions	Directed hunting occurred at the haulouts south-east of Belkofski, which was the traditional hunting territory and harvesting location for the Aleut of the now abandoned village of Belkofski. The people of Sanak Island traditionally harvested sea lions at the haulouts south of Sanak and at Clubbing Rocks and Cherni Island (Fig. 1), while the peoples of Ikatan and False Pass hunted a number of haulouts around the Ikatan Peninsula	Interviews
Nelson Lagoon, False Pass, Akutan	Interactions	Those living on the north shore of the western Peninsula hunted at Amak Island. The Aleut of Belkofski, Sanak Island, Ikatan Peninsula (Unimak Island) and False Pass regularly harvested sea lions for food until the 1960s, but the Amak Island area has not been hunted for nearly a century	Interviews
King Cove	Causes for Decline	Aleut fishermen stated, 'Instead of chasing salmon and herring which are real oily and rich fish, they are chasing pollock and cod. We think – I think, and I'm not the only one – that they are starving with full bellies. No oil and no fat in cod and pollock, very little. They are starving to death with full bellies Yeah, there were hundreds and hundreds and thousands of sea lions (in the 1950s and 1960s) from here all the way to the Aleutians. They've only started to disappear after the cod and pollock came into being. It is all just a natural cycle and they can't blame fishermen for sea lions aren't eating them. The sea lions that are eating salmon are probably living'	Interviews
King Cove	Causes for Decline	'If they starved, we would have found them (their carcasses). Look for the damned killer whale scat'	Interviews
Sand Point, King Cove	Causes for Decline	Are fisheries the cause? Local levels of commercial harvest near sea lion rookeries and haulouts were trivial compared with the catches of large ships offshore, or even those from the American west coast	Interviews
False Pass, Nikolski	Causes for Decline	Food? Elders pointed out that gadids often disappear for extended periods and that this affects the mammals that eat them. Long-term population fluctuations in cod and pollock are poorly understood, but were noted in the Aleut language. As recorded by Lydia Black referring to a conversation held in Unalaska in 1978, 'Fr. Paul Merculief, a native of St. George Island and a resident of Nikolski, Umnak Is., pointed out that the Aleut term for codfish can be rendered into English as "the fish that stops", meaning it disappears periodically'	Interviews and Black (1981)



**Figure 2** (a) The 5000-year distribution of percentage number of individual specimens (NISP) identified for each category or taxa. (b) Long-term trends in the relative numbers of Steller sea lions and sea otters harvested over the last 4500 years as measured by the Abundance Index with sea otter as the low-ranking taxa, phocidae as the low-ranking taxa and sea otter calculated against phocidae. This demonstrates an inverse relationship between Steller sea lion and sea otter [Spearman correlation coefficient (rho) = -0.73]. (c) Long-term trends in the relative numbers of all identified Otariids and Phocidae as measured by the Abundance Index with sea otter as the low-ranking taxa. Fur seal is also calculated against sea otter as the low-ranking taxa for comparison. Otariidae and Phocidae co-vary in time [Spearman correlation coefficient (rho) = 0.87]. All Lowess curves weighted at 40%, data from Table 1. Grey bars are the cooler intervals identified in Table 2.

record were due to changes in the technological capabilities of the Aleut inhabiting the region. For example, there is no evidence from the taxa being harvested of major changes in boating technology over the last 4500 years. However, changes in harvesting technology often reflect changes in access to certain mammals as shown by the large-bladed thrusting spears that were used to hunt sea lions on the beach, while short end-blades and toggling harpoons were used to hunt smaller sea mammals such as phocids in the open water. A plot of spear point length through time presents a

Lowess curve that corresponds closely with the early peak in sea lions before 3600 years ago, the lack of shore-bound sea lions near villages from 3300 to 1400 years ago, followed by an expansion 1400 years ago, another decline during the Medieval Climatic Anomaly 1000–700 years ago, and a return to shores near Aleut villages 700 years ago (Fig. 3). The d15N values from Aleut burials (which reflect the Aleut diet in the Umnak region) show a similar trend and suggest that high trophic feeding sea mammals declined as an important part of the diet from 3600 years



**Figure 3** Trends in projectile point length plotted for the last 6000 years. Large projectiles for thrusting spears are a measure of access to shore-bound sea mammals. Here, we see that during the Neoglacial early in the sequence, and during the Little Ice Age, there appear to have been greater access to shore-bound sea mammals. During the period from 3600 to 1500 years ago, there was less access. These data also track the d15N and human population data in Figs 4 and 5.

ago. Over the next 3000 years, the period of decreasing spear point size, d15N values decreased and rose again rapidly in the Little Ice Age (Fig. 4), indicating a rapidly expanding population of large, shore-bound sea mammals, which were most likely SSL – a trend noted in the archaeological remains by Yesner (1981, 1988) and one that closely tracks the Steller sea lion to sea otter abundance index superimposed over the data in Fig. 4.

While it is impossible to use archaeological data to determine absolute abundances of individual species, the thousands of bones from archaeological sites allowed us to reconstruct relative abundances because the ancient Aleut, like most foragers, tended to harvest taxa in numbers relative to their actual abundance on the landscape (Yesner 1981; Betts 2000). In effect, their procurement strategies reflected the natural productivity of their surrounding ecosystem. Substantial changes in the proportions of Steller sea lion or sea otter bones should indicate actual changes in the proportions and availability of these animals on the natural landscape. Centennial scale changes in species abundance are a measure of long-term and region-wide fluctuations in the marine environment.

The evidence that sea lion populations declined (and increased again) prior to the development of industrialized fisheries, as recorded in deep time, the ethnohistoric record, and in the oral histories of living people, leaves three options to explain the historic changes noted in sea lion abundance (following Charnov et al. 1976). First, the changes in sea lion abundance, particularly the decreases, could have been caused by natural sources of mortality such as disease or predation by killer whales. Second, the changes could be related to exploitation by humans (anthropogenic effects), and finally, the changes in sea lion abundance might be explained by natural changes in ocean climate that shifted marine productivity and affected the microhabitats and resources available for sea lions.

#### Non-human predation

Over 90% (47 of 52) of the Aleut interviewed felt that predation by killer whales was the ultimate cause of the most recent Steller sea lion decline. Predation by killer whales on SSL was noted by many early explorers including Nelson (Nelson 1887) who stated that like the fur seal they have a dreaded enemy in the killer whale', although for more than a century before this time, we found no



**Figure 4** The d15N values for 80 human burials from the Umnak Island region in the eastern Aleutian Islands showing a downward trend in the consumption of high trophic feeders (otariids) from 3500 years ago to 1000 years ago, and then a rapid increase in the Little Ice Age (data from Joan Coltrain *et al.* 2006). The Steller sea lion to sea otter abundance index (AI) is plotted over the d15N values to show that broad changes in the use of higher trophic level species as measured by d15N, track the overall trends in the abundance of Steller sea lion.

mention by Russian observers of interactions between SSL and killer whales. The fact that SSL were in deep decline in the 1870s (see above), and that killer whales were observed preying on them as well, may be more than coincidence as it mirrors the patterns of change 100 years later.

Killer whales have recently been investigated for predatory attacks on sea lions (Heise et al. 2003; Springer et al. 2003; Trites et al. 2007b; Wade et al. 2007; Horning and Mellish 2012). The Aleut proposed this hypothesis to the US National Marine Fisheries Service in the late 1980s and provided a video of killer whale attacks on Steller sea lion rookeries. Fishermen report today that killer whales have expanded their range into Bristol Bay where many local people have fished for 50 years - but it is only in the last 10 years that killer whales have been seen there. Incidences of predation on sea lions were noted in the Gulf of Alaska and eastern Aleutian Islands from the 1950s through the 1990s. In 2003, a giant pod of killer whales was repeatedly spotted moving through False Pass. Estimated numbers by local fishermen ranged from 200 to 400 individuals. There was general consensus that there were no seals, sea lions or sea otters in the area after they left.

Predatory attacks on sea lions by killer whales in the Aleutian Islands have received considerable research attention over the past decade (Heise et al. 2003; Springer et al. 2003; Trites et al. 2007b; Wade et al. 2007; Durban et al. 2010). Field observations of killer whales in the eastern Aleutian Islands reveal that there are three types of killer whales - one form that only eats fish (residents), one that eats only marine mammals (transients) and a third with an uncertain diet (offshores; Matkin et al. 2007). A minimum of 165 transients, 901 residents and 54 offshore killer whales were photographically identified from 2001 to 2004 in the eastern Aleutians. The fisheating killer whales outnumbered the marine mammal eaters by a factor of 6 and were seen 12 times more frequently (Matkin et al. 2007). Subsequent estimates suggest a total population of 345 transient killer whales occurring in seven distinct clusters across the Gulf of Alaska and Aleutian Islands (Durban et al. 2010). Thus, the large pods of killer whales reported by the Aleut likely consisted of the fish-eating form given the numbers reported and the fact that the fish-eating and marine mammal-eating groups of whales do not intermix. Documented predation events suggest that the preferred prey in the eastern Aleutian Islands are grey whale calves and NFS, and not sea lions (Matkin *et al.* 2007). Mathematical models further suggest that killer whales were unlikely to have caused the recent decline of sea lions, but could be a significant factor after the sea lion population had fallen to low numbers (Guénette *et al.* 2006, 2007). More recent observations suggest that killer whales may also be the largest impediment to population recovery (Horning and Mellish 2012).

## Disease

The magnitude of population collapse exhibited by SSL over the past four decades should have resulted in considerable numbers of carcasses if disease was the underlying cause of their decline. But this was not the case. Even at the rookeries and haulouts, local people saw very few dead sea lions - reporting seeing fewer than 10 dead sea lions at rookeries and haulouts over the last 50 years. Although dead SSL are more likely to sink than most marine mammals, Elliot (1886) suggested that this is a summer phenomenon when they have less fat (cf. Veniaminov 1984). The 200 000 missing sea lion carcasses should have left a considerable visual and olfactory impact on the landscape if they had died of disease.

Every Aleut fisherman or elder interviewed stated they have either never seen a Steller sea lion carcass or only seen a few in their lifetime of fishing and beach combing, even at the rookeries and haulouts. One 70-year-old elder, who trapped and fished the entire Alaska Peninsula region for 55 years, had seen 4 in his lifetime. That was more than anyone else in our surveys reported (more than 75%, n = 40) had never seen one). In the 1830s, Veniaminov (1984) observed that, 'A sea lion which is killed in the water sinks at once. The body floats only when its insides begin to rot'. Nearly all Aleut fishermen asked a similar question, summed up by one observation: 'the dead eventually float – where are the bodies?'

Blood samples taken from SSL since the 1970s indicate that sea lions were exposed to a wide number of diseases in regions where sea lions declined as well as in regions where sea lions increased (Burek *et al.* 2003, 2005). However, the blood samples and field observations revealed no evidence of an epidemic or other significant expo-

sure to diseases that could have caused sea lions to decline in the Gulf of Alaska and Aleutian Islands – a conclusion substantiated by the overall paucity of local observations of dead sea lions in the regions occupied by the Aleut.

# Anthropogenic effects: fisheries competition, human predation

Aleut interactions with SSL come in two primary forms - passive observation and not so passive interactions while fishing or hunting. Recent Aleut interaction with sea lions was relatively passive while the Aleut fished around Steller sea lion rookeries and haulouts, especially in the last 50 years when SSL played little role in the subsistence economy. Fishing is now restricted in many areas where observations used to occur. But passive observation does not imply benign interactions. Aleut fishermen spend extended periods of time on their boats at sea, making frequent observations of SSL. Sea lions are largely regarded as dangerous pests, following boats, picking fish out of nets, threatening and even succeeding in pulling fishermen off the decks of their boats (Table 4).

Unfortunately, we cannot corroborate the short temporal relationships and observations from Table 4 with the longer-scale archaeological data. much like the case with comparing historical fish harvests with long-term palaeoecoloigcal data sets (Finney et al. 2010). When studying long-term trends, it is also difficult to relate the decreases in sea lion abundance (as measured by the Abundance Index – AI) to human exploitation pressure (overexploitation). Under normal conditions, exploitation pressure should have increased with increases in human population size such that fewer sea lion bones should have been recovered from middens when human populations were high compared with when they were low (Grayson 2001; Betts and Friesen 2006). Yet the opposite appears to have occurred.

In our study area, human populations rose slowly and predictably throughout the Neoglacial as a general trend, but there were a number of periods of population expansion and contraction (Fig. 5a–b). In general, human populations rose during cooler climatic regimes and declined during warmer climatic regimes, both in the single island example (Fig. 5a) and across the entire North Pacific (Fig. 5b). Comparing this model of human population fluctuation and growth to the Abundance Index for SSL shows an interesting pattern (Fig. 2b,c) when superimposed over Fig. 5a. An inverse relationship should have occurred between otariid abundance and human population size if AI fluctuations were associated with hunting pressure. Instead, the relative abundance of SSL appears to have been independent of human population trends, and the two curves closely track each other. The implication is that hunting did not regulate the size of Steller sea lion populations [though, it undoubtedly influenced the sea lion behaviour in relation to humans (Betts *et al.* 2011)] and that the conditions regulating Steller sea lion abundance might be the same factors regulating human populations (see below).

The Aleut and the Steller sea lion have shared a common geography for thousands of years (the earliest known occupation in the eastern Aleutian Islands is about 9800 years ago), but have had limited interactions over the last 40 years as fisheries restrictions were imposed and subsistence hunting declined. Approximately 30 000 Aleut were estimated living in the region 400 years ago (Federova 1973; Lantis 1984; Veniaminov 1984; H.D.G. Maschner unpublished archaeological data), and all archaeological data from the region indicate that thousands of sea lions were taken each year by the Aleut prior to the 1900s to meet their basic caloric needs (Denniston 1973; Yesner 1977).

Beyond a food source, SSL likely played another essential role in the lives of the Aleut. Michael Livingston, an Aleut and master kayak builder, experimented with kavak construction in the Aleutians and found that the skin of the Steller sea lion is the only skin that works efficiently for covering baidarkas (kayaks; M. Livingston, unpublished data and personal communication). While skins from phocid seals could be used (requiring a greater number of animals and much more energy to obtain them and remove the hair), there is no evidence that the peoples of the Aleutians ever considered small seals as a viable source of kayak covering. Historically, each adult male Aleut owned at least one kavak, which took five to six Steller sea lion skins to cover, and needed to be replaced every year (according to experiments by Livingston). As the kayak was the only means for the Aleut to hunt and fish, SSL would have amounted to a 'fixed cost', meaning that regardless of the number of SSL on the North Pacific, the Aleut harvest would have ultimately been dictated



**Figure 5** (a) The Human Occupation Index for Sanak Island spanning 5000 years as created by Joseph Cornell (Maschner *et al.* 2009a), based on house floors, village area and radiocarbon distributions. Periods of population expansion co-occur with cooler climatic regions at 5600–5400, 3800–3600, 2400–2200 and 650–350 years ago. Population decline is found during warmer regimes 4400–4100, 3000–2700, 1900–1700 and 900–700 years ago. The one out-of-pattern event is 1400–1100 years ago, a period of expanding salmon populations and variable climate (see Finney *et al.* 2002, 2010). The Steller sea lion to sea otter abundance index (AI) is plotted over the population chart to show that except for the one out-of-phase population increase after 1400 years ago, trends in Steller sea lion and human populations appear to co-vary. (b) 1024 radiocarbon dates for the region from the Kenai Peninsula to the western Aleutian Islands showing that the micro-regional pattern in population growth and contraction seen on Sanak Island (Fig. 5a) is a subset of a macro-regional pattern spanning the North Pacific.

by the number of Aleut males owning kayaks, and not by the number of sea lions actually on the landscape. Thus, the 3000–4500 adult male Aleuts we estimate were present between AD 1400 and 1700 in the Aleutians would have required between 12 000 and 27 000 SSL each year just to cover their kayaks. These numbers were presumably harvested at sustainable levels for hundreds of years. The reduction in Aleut populations from disease and the colonization and technological introductions by Europeans altered their demand for sea lions as a clothing and boat covering material and would have significantly reduced the numbers taken for consumption during the 1900s. Our field and literature research on western Gulf of Alaska communities found that a mere 1.0% of Sand Point households and 1.3% of King Cove households used SSL in 1992, although none reported actually hunting them (Fall et al. 1993); while only one False Pass household reported harvesting a sea lion in 1987-1988, none reported any Steller sea lion harvest or use in 1992-1995 (Wolfe and Mishler 1993: Fall et al. 1996). Annual surveys by the Subsistence Division in Sand Point and King Cove found that between 1998 and 2008, Sand Point averaged approximately 1.7 sea lions per year and King Cove 1.9 per year. A 2010 survey of Akutan, False Pass and Nelson Lagoon found that only Akutan had harvested three SSL in the previous 18 months (K.L. Reedy-Maschner, unpublished survey data). In the 1990s, there were few instances of SSL being shot, and as noted by Stewart (1999), if there had been shootings, village politics are such that someone would have reported it. Overall, human-caused mortality appears to have decreased during the period of declining Steller sea lion numbers.

During the 1940s, a number of the people we interviewed had watched or participated in Navy target practice exercises that used SSL as targets during WWII (Cherni Island, Clubbing Rocks and south Sanak). This was followed by a governmentsanctioned experimental commercial harvest of 630 sea lion bulls in 1959 that proved uneconomical (Thorsteinson et al. 1961), and a sea lion pup harvest from 1963 to 1972 during which 45 000 animals were taken for their pelts (ITG 1978). All of these government-sanctioned control measures and harvests were stopped in 1972 with the enactment of the US Marine Mammal Protection Act. Interestingly, Steller sea lion populations were growing during this period despite all of the actions taken to remove them or reduce their numbers (Trites and Larkin 1996).

Trites and Larkin (1992) estimated the numbers of sea lions shot or drowned through subsistence and fishery takes since the 1950s. They concluded that the numbers killed probably rose from a level of 1500 animals per year in the late 1950s to a peak of around 4000 animals in the early 1980s. They also felt that human-caused mortality likely decreased through the late 1980s as the sea lion population declined and public attitudes towards sea lions changed. Discussions with fishermen suggested to Trites and Larkin (1992) that many fishermen became aware of the seriousness of the sea lion population decline in the late 1980s and modified their behaviour because of the political and economic ramifications of shooting sea lions. Numbers of sea lions taken by fisheries and subsistence hunts was estimated to be about 500 animals per year in the late 1980s and early 1990s (Trites and Larkin 1992) and fell to about 200 annually in recent years (Trites *et al.* 1999, 2007c; Turek *et al.* 2008). These numbers represent a small percentage of what the Aleut took historically and are unlikely to have had a measurable effect on sea lion population numbers, but it is not known whether different ages and sexes of sea lions were targeted in the different time periods.

The historic pattern of human population size over the past 4500 years (excluding the past century) showed periods of increases and decreases similar to the sea lion abundance indices. At no point were the patterns of change in sea lion numbers consistent with a model of over-exploitation. A similar analysis by Savinetsky et al. (2004) from archaeological materials in the Bering Sea also found no relationship between hunting and marine mammal abundance over the past 2000-3000 years. Indeed, the correspondence between human population and Steller sea lion abundance suggests that both human and sea lion population fluctuations were correlated with climatic changes and consequent changes in marine productivity in the same way (discussed below). We believe that the notion of fixed costs for kayak construction certainly lead to a strong ecological relationship between human populations and the numbers of harvested sea lions. But we also note that changes in marine productivity may have driven both and that a climate caused decline, combined with the need to maintain harvests for boat building, probably had cascading effects.

# Environmental change

There is mounting evidence that SSL responded dramatically to shifts in marine productivity during the 1900s caused by punctuated changes in ocean climate (regime shifts) that occurred on decadal timescales (e.g. Trites *et al.* 2007c; and Table 3). The same pattern also appears to occur on a coarser scale in the archaeological record whereby relative abundances of SSL over the past 4500 years (Fig. 2a–c) correspond to the model of climatic change detailed in Table 2.

The role of regime shifts in the structure of the North Pacific ecosystem has become an important

aspect of the dialogue in attempting to understand fluctuations in the abundance of a number of species, and the Steller sea lion is no exception (Mantua et al. 1997; Trites et al. 1999; Benson and Trites 2002; King 2005). Trites et al. (2007c) make a strong case for shifts in ocean climate being the critical factor in the Steller sea lion decline. Over the past century, large-scale shifts occurred in climatic and oceanic conditions in 1925, 1947, 1977, 1989 and 1998. The shifts appear to have occurred abruptly and were not random variations or simple reversals to previous conditions. The period from 1947 to 1977 appears to have been one when sea lions increased in abundance while consuming a higher proportion of fatty fishes such as capelin (Mallotus villosus), herring (Clupea pallasii) and sand lance (Ammodytes hexapterus). In contrast, the period following the largest oceanic regime shift of the 1900s in 1976-1977 was followed by a decline in sea lion numbers and an increase in the abundance of leaner fishes such as Pacific cod, walleye pollock and Atka mackerel (Pleurogrammus monopterygius). Both of these shifts are highlighted by reconstructions of the Pacific Decadal Oscillation - PDO (e.g. Biondi et al. 2001).

It is postulated that sea lion pups have a limited stomach capacity and cannot obtain sufficient calories to meet their daily needs from a diet dominated by lean species of fish. An ecosystem dominated by cod, pollock or Atka mackerel could thus delay the age at weaning by 1-2 years until the relative energy requirements of young sea lions are low enough to be met by the available prey base (Alverson 1992; Rosen and Trites 2000, 2004, 2005; Trites and Donnelly 2003). Such a scenario would reduce birth rates (as females forego pupping to successfully wean their young) and cause the sea lion population to decline (Trites et al. 2006). Population recovery is thus likely linked to consuming a more diverse range of species with higher fat (energy) contents than sea lions are currently obtaining, as suggested by the correlation between diet diversity, energy density and the rates of historic sea lion population change (Merrick et al. 1997; Trites et al. 2007a).

The 1977 regime shift has been well documented scientifically (e.g. Ebbesmeyer *et al.* 1991; Miller *et al.* 1994; Anderson and Piatt 1999; Hare and Mantua 2000; Benson and Trites 2002; McGowan *et al.* 2003), and by the local Aleut community who noticed the return of gadids and the decline of the Steller sea lion. The local communities were also quite aware of the regime shift that occurred in the 1940s that saw the disappearance of cod in many areas of the Alaska Peninsula, and the expansion and success of Steller sea lion populations. All of the people we interviewed who commented on this (n = 3, all >75 years old) became aware of the major change taking place between 1942 and 1945 (Table 2) and reported that large numbers of SSL appeared after the collapse of the cod stocks in the early 1940s. They also reported that the Steller sea lion began to decline just as the cod came back and became a viable commercial enterprise.

Stewart (1999) similarly remarked that the people of Akutan 'associate this decline (of sea lions), as do people in False Pass, King Cove and Sand Point, with a decline of, what they call locally, candle fish. This would be referred to by scientists as capelin. 'They are called candle fish because when you dry them, it just takes a few of them lit by a match to start a fire with wet driftwood on the beach. We have no trees in the area so you burn whatever it is that floats ashore. Candle fish are a high fat item and a prized survival species for people in the region'. All of these events appear to correlate with the reported regime shifts in the North Pacific ecosystem.

In reference to the decline of sea lions that occurred following the major regime shift of 1976-1977, Stewart (1999) noted that 'it is not the first time they (the people of Akutan) have seen a decline in SSL in the region, and they certainly don't expect it to be the last time'. The oral and written records indicate that a similar collapse of SSL occurred throughout the Aleutians Islands and Gulf of Alaska about 100 years earlier in the 1870s (implications described above, Table 3) during an apparent warming period as identified in air temperatures recorded in Sitka, Alaska [see T.C. Royer, personal communication, as cited in Trites et al. (2007c) and measured in the PDO by Biondi et al. (2001)]. We believe it is also noteworthy that the timing of this population decline corresponded with the start of the Scandinavian migration that was drawn to Alaska to catch the abundant gadids (a fishery that lasted until the late 1930s; Table 3). Memories recorded by Miriam Weissinger (1961) following a stay on Adak Island were also particularly insightful in understanding the sea lion decline when she wrote that the 'cod were almost unknown until the sea lion herds diminished in 1873; now they are very common. The Atka mackerel was unknown on Attu before 1875, when it appeared unexpectedly. The natives say that it drove the sea lions away'. Collectively, these observations recorded long before the present decline of sea lions appear to parallel modern-day observations.

The archaeological record of marine productivity extends further into the past and points to perisho of increased and decreased marine productivity that are concurrent with changes in climate and sea lion abundance (comparing Tables 1 and 2, and Figs 2a,b and 6a,b). Most notably there was (i) low Steller sea lion frequencies at the end of the middle Holocene, a warm period; (ii) an increase in sea lion frequencies during the cooler Neoglacial conditions after 4000 years ago; (iii) an apparent depression in frequencies during a suspected warmer interval about 2700 years ago; (iv) a rise in numbers after another cooler episode that began 2400 years ago; (v) a slight sea lion resource depression beginning 1800 years ago and extending through the Medieval Climatic Anomaly to at least 700 years ago; and (vi) increases in sea lion frequencies associated with the cold temperatures of the Little Ice Age that began 600 years ago. These data also track other reported changes in the long-term marine productivity of the North Pacific (Finney et al. 2002; Misarti 2007; Misarti et al. 2009).

A notable change in marine productivity occurred during the Medieval Climatic Anomaly between 700 and 900 years ago (and perhaps stretching back to 1200 years ago) when marine productivity is believed to have been reduced in the Gulf of Alaska and Aleutian Islands (Finney et al. 2002; Maschner et al. 2009b; Misarti et al. 2009). The few archaeological samples that are available from coastal village sites for this period [due to a catastrophic reduction in human populations (Maschner et al. 2009b)] contained few seals and sea lions, but high frequencies of sea otters, a very poor nutrition food that was increasingly filleted during warm periods (Lech et al. 2011). This is significant because the sea otter was not considered food by the Aleut in the nineteenth century (Veniaminov 1984) or in the modern day (Reedy-Maschner unpublished data). Instead, it appears that the Aleut only moved to smaller and smaller mammals, eventually harvesting sea otters, during periods of dietary stress. This dietary shift by Aleuts to otters 1000 years ago may have a parallel with the apparent shift in diets of some killer whales to otters in the last 20 years (Estes *et al.* 1998; Bernard *et al.* 2011).

The preserved coastal midden deposits appear to be scarce during the Medieval Climatic Anomaly because most village sites were located away from the coast on small salmon streams during this period of oceanic warming and reduced primary productivity. The fact that the few village sites that remained on the outer coasts were dominated by sea otters, caribou (Rangifer tarandus) and salmon (Maschner, unpublished) implies that some shift must have occurred in the North Pacific ecosystem to cause the prehistoric inhabitants of the region to shift their diets to lower-ranked species. In contrast, the trends in the late Holocene suggest that the Neoglacial was likely beneficial climatically for Steller sea lion populations in the Gulf of Alaska and Aleutian Islands. Further north in the Bering Sea. Savinetsky et al. (2004) studied bones from various archaeological sites and concluded that population changes of SSL and other marine mammal species also correlated with environmental conditions (temperature, precipitation, ice cover and sea level changes). They also concluded that most marine mammals maintained their overall geographical distributions during the past 2000-3000 years, but experienced changes in abundance.

# Synergies

While the declines noted in the 1870s and 1980s are consistent with shifts in ocean climate towards warmer conditions, the declines of sea lions could have also been driven faster and further by the synergistic effects of human hunting and predation by killer whales. The North Pacific was 150 years into the commercial sea otter harvest when the 1870s' regime shift occurred. At this time, the Aleut population was lower than it had been in 4000 years, but hunters were spending considerable time on the North Pacific waters seeking the few remaining sea otters. Based on experiments conducted in the construction and repair of traditional style kayaks, Michael Livingston (personal communication) estimates that Aleut hunters may have needed to replace their kayak skins three or four times per year at this time because of the inordinate distances travelled and the time spent hauling boats on beaches, thereby perhaps equalling the harvest of SSL prior to human depopulation of the region. It is possible that the equilibrium that had been maintained with the sea lion populations could no longer be maintained when the warming climatic conditions occurred and could not be re-established. Killer whales could have in turn exacerbated the problem once the sea lions had been reduced to low numbers as shown by the mathematical models of Guénette *et al.* (2006, 2007).

The extremely rapid decline that occurred through the 1980s corresponds with the largest shift in ocean climate conditions recorded during the twentieth century, which affected suites of species in the North Pacific (Benson and Trites 2002). However, the 1980s was also the decade when the largest numbers of sea lions were removed by shootings and entanglement by fisheries in some parts of Alaska (Trites and Larkin 1992). Thus, anthropogenic mortality compounded by predation by killer whales could also have driven sea lions in some regions of Alaska to lower numbers faster and further than would have occurred under natural conditions. Such a scenario could also have played out 1200-700 years ago in the prehistoric sequence when a climatic regime shift resulted in a significant resource depression after nearly 1000 years of equilibrium and human harvesting. In all these scenarios, we note that humans could well have been contributing forces in the sea lion trends, but that the ultimate driving force lies with a regime shift in ocean climate, not human exploitation. We also note that the late 1800s' declines of sea lions ushered in the greatest commercial cod fishery of the nineteenth century, only rivalled by the cod and pollock fisheries of the late twentieth century that continue today.

Beyond basic subsistence needs, we suspect the Aleut also applied a large selective force on Steller sea lion populations over thousands of years of harvesting. Anthropologists and archaeologists have assumed for many years that the reason the Steller's sea cow (*Hydrodamalis gigas*) was found in the one Aleutian region never colonized by the Aleut is because early on they were harvested to extinction by the initial colonists in the rest of the Aleutian region (Domning *et al.* 2007; Byers *et al.* 2011). It is therefore noteworthy that the youngest dated sea cow remains were recently found in the western Aleutians (on Buldir Island), which was one of the remotest locations to be harvested

by the Aleut (Corbett et al. 2008) and one of the last places to be colonized. Using this as an anecdotal measure of Aleut - marine mammal relations, it should also come as no surprise that SSL, which are wary of humans, spend most of their time in relatively inaccessible locations while fur seals, which have only had direct land-based contact with humans since the forced relocation of the Aleut to the Pribilof Islands 200 years ago, have less fear of humans. Thus, 10 000 years of harvesting has likely created the 'natural' Steller sea lion behavioural ecology seen today. The zooarchaeological data we have presented, particularly the trends evident before 2500 BP, may track these behavioural changes in sea lions. Steller sea lions thus likely adapted to human predation by adopting new and more remote rookeries and haulouts, especially during periods of population decline, and likely returned to the larger and more accessible islands during periods of increase (Betts et al. 2011).

The expansion, contraction and expansion of Steller sea lion populations over thousands of years is documented in the technology used by North Pacific peoples to harvest large sea mammals. The transition from thrusting spears to darts is a proxy measure of a reduction in accessible shore-bound large sea mammals. The reintroduction of thrusting spears 1400 years ago and again during the Little Ice Age 600 years ago (but missing in the MWP) is a measure of a renewed access to these resources (Fig. 3). This same pattern is reflected in the d15N values on human remains from the Umnak Island area, indicating that earlier abundances before 3600 years ago, followed by a decline through the Medieval Climatic Anomaly, and a massive increase in higher trophic level foods during the Little Ice Age 600-400 years ago (Fig. 4) can be replicated in multiple data sets. Human populations directly track these trends (Fig. 5a,b).

The archaeological data from ca. 4500 to 3500 BP suggest that Steller sea lion populations rapidly colonized the lower Alaska Peninsula as coastlines stabilized from glacial rebound during a climatic optimum (the Neoglacial) and were subsequently intensively exploited by human hunters (Betts *et al.* 2011). The sharp decline ca. 3000 BP may represent the movement of sea lions to inaccessible rookeries and their learning to avoid human predation and may have been followed by a sort of equilibrium between local

populations and humans during a relatively stable climatic period (Betts et al. 2011). Following 2000 BP, Steller sea lion populations appear to have closely reflected trends in climate and oceanic productivity. It should be kept in mind, however, that these colonization events and behavioural adaptations likely occurred much more rapidly than the coarse centennial timescales covered by our data. One important caveat is that we have no regional data for the first half of the Holocene, but Betts et al. (2011) showed that for a single island colonized only 6000 years ago, similar patterns can be identified. We also recognize that these patterns are quite different from more southerly regions such as the California Coast where the early extirpation of otariids from island rookeries and haulouts had catastrophic effects on those populations (Rick et al. 2008: Braie 2010: Erlandson and Rick 2010: Braje et al. 2011).

After thousands of years of intensive Steller sea lion harvesting in the North Pacific, the 1960s saw little evidence of human-caused mortality. Steller sea lions were no longer hunted extensively for food and materials except in a few communities and at very low numbers, and the Navy no longer used them for target practice. These factors in combination with the regime shift in the late 1940s (that would have reduced the abundance of gadids and increased the abundance of oily fishes) could have contributed to SSL reaching the highest numbers recorded in the twentieth century. Sea lion numbers were extremely high during the 1960s and 1970s, but could not be maintained when faced with the 1977 regime shift and the influx of less nutritious prey in the form of gadids and Atka mackerel that returned to dominate the ecosystem.

# Conclusions

Humans have been an integral part of the Alaska marine ecosystem for thousands of years, and there is no *a priori* reason to assume that the North Pacific ecosystem can be understood without reference to the role that humans have played (or continue to play) in that ecosystem (Maschner *et al.* 2009a). The southern Bering Sea and North Pacific should be seen as a complex system: an ecological system that functioned for more than 10 000 years with the Aleut actively harvesting the marine environment. The indigenous peoples of the region are not separated or disjointed from the ecosystem – they were and continue to be an integral part of it and should be considered as agents in the structure of northern ecosystems.

Our study suggests that humans were likely a significant but not dominant force in the prehistoric natural history of SSL. The strongest relationships we observed with changes in Steller sea lion abundance were related to climatic regime shifts at the end of the Holocene and not to human predation. We could not directly relate declines in Steller sea lion abundance over the last 4500 years to human exploitation, although natural declines of sea lions caused by shifts in ocean climate could have been further compounded by the synergistic effects of humans and killer whales removing individuals from declining populations. Human data (populations, technology and diet) proved to be a useful proxy to investigate the effects of climate on Steller sea lion abundance. Most notably, it shows the utter dependence of the Aleut on sea lions (to cover their kayaks) to fully exploit the marine ecosystem - thereby suggesting that humans and Steller sea lion populations likely adapted to one another through changes in behaviour and natural history and maintained modest equilibrium before the punctuated major climactic regime shifts occurred during the Medieval Climatic Anomaly and the Little Ice Age, as shown by our archaeological data (Betts et al. 2011).

Archaeological data provide information about the structure of prehistoric ecosystems and the kinds of long-term patterns of spatial and temporal variation that are present in these systems, while ethnohistoric data and traditional ecological knowledge of local Aleut fishermen provide information about changes in the marine ecosystem that occurred on decadal scale spanning nearly 200 years. Collectively, these data indicate that declines in sea lion abundance occurred during periods of hemispheric warming and altered oceanic productivity over the past 4500 years. There was at least one major collapse of the North Pacific ecosystem approximately 700-1100 years ago, and a more recent decline of sea lions in the 1870s that led to widespread starvation for the indigenous peoples who depended on them. These data suggest that the greatest densities of SSL occurred during cool periods and are consistent with the ocean climate hypothesis (Trites et al.

2007c) proposed to explain the most recent decline of sea lions in Alaska.

All of the changes noted in sea lion abundances across the different spatial and temporal scales were associated with major shifts in ocean climate conditions. Densities of SSL were higher during the cool periods of the Neoglacial, the Little Ice Age and the mid-twentieth century and were lower during the warmer periods of 3000 years ago, the Medieval Climatic Anomaly, the late nineteenth century and late twentieth century. Human harvesting of SSL should be considered part of the natural ecology of the SSL, much as predation by killer whales is readily recognized as being part of it. Archaeological and anthropological analyses provide data for timescales that are currently not available in any other form of analysis. They demonstrate that the North Pacific and southern Bering Sea have been dynamic, volatile and subject to great fluctuations over the past hundreds to thousands of years. This requires careful re-evaluation of current models of sustainability for marine ecosystems to determine where Alaska is positioned in the 21st century within one of the large naturally occurring cycles.

# Acknowledgements

This research was primarily funded by a grant from NOAA through CIFAR at UAF (CIFAR 06-047) to Maschner and Reedy-Maschner. This generous award allowed us to conduct research that was community based and founded in research questions instigated at the local level, and we gratefully acknowledge the support of CIFAR and NOAA throughout this project. Earlier, concurrent or later projects that contributed data include Maschner's NSF awards OPP-0137756, OPP-9996415, OPP-9996372, BE/CNH 0508101, BE/ CNH-0119743, Reedy-Maschner's OPP-0094826, USF&W Office of Subsistence Management' FIS02-032. and BOEM contract M08PC20053. Dr L. Ford, former Vice President of Research at Idaho State University, provided generous postdoctoral support for a portion of the research in this paper. Peter Pan Seafoods has contributed to project logistics for many years and we gratefully acknowledge their support. We are also grateful for the support provided to A.W. Trites by the North Pacific Marine Science Foundation through the North Pacific Universities Marine Mammal Research Consortium. We acknowledge the work of all of the students who processed the remains summarized in this study, but especially Amber Tews and Veronica Lech. Michael Livingston, Aleut and Master kayak builder, was generous in providing details of kayak construction and Steller sea lion skins. We have incorporated many of the suggestions of six anonymous reviewers and appreciate their contribution to this work. Of course, this project could not have been done without the extensive contributions of the people of the region, particularly those in the communities of Sand Point, King Cove, False Pass, Nelson Lagoon, Akutan and the greater Aleutians East Borough.

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