UC San Diego
UC San Diego Previously Published Works

Title

Stable isotope values in pup vibrissae reveal geographic variation in diets of gestating Steller sea lions Eumetopias jubatus

Permalink

https://escholarship.org/uc/item/2qm0624h

Authors

Scherer, RD
Doll, AC
Rea, LD
et al.

Publication Date

2015-05-07

DOI

10.3354/meps11255

Peer reviewed

Stable isotope values in pup vibrissae reveal geographic variation in diets of gestating Steller sea lions *Eumetopias jubatus*

Rick D. Scherer[1,8], Andrew C. Doll[1,*], Lorrie D. Rea[2,3], Aaron M. Christ[2], Craig A. Stricker[4], Briana Witteveen[5], Thomas C. Kline[6], Carolyn M. Kurle[7], Michael B. Wunder[1]

[1]Department of Integrative Biology, University of Colorado Denver, Denver, CO 80204, USA
[2]Alaska Department of Fish and Game, Division of Wildlife Conservation, Anchorage, AK 99518, USA
[3]Institute of Northern Engineering, University of Alaska Fairbanks, Fairbanks, AK 99775, USA
[4]US Geological Survey, Fort Collins Science Center, Denver, CO 80225, USA
[5]Kodiak Seafood and Marine Science Center, University of Alaska Fairbanks, Kodiak, AK 99615, USA
[6]Prince William Sound Science Center, Cordova, AK 99574, USA
[7]Division of Biological Sciences, Ecology, Evolution, and Behavior Section, University of California San Diego, La Jolla, CA 92093, USA

[8]*Present address:* Conservation Science Partners, Fort Collins, CO 80524, USA

ABSTRACT: Multiple factors, including limitation in food resources, have been proposed as possible causes for the lack of recovery of the endangered western segment of the Steller sea lion population in the United States. Because maternal body condition has important consequences on fetal development and neonatal survival, the diets of pregnant females may be particularly important in regulating population sizes. We used the stable carbon and nitrogen isotope values of vibrissae from Steller sea lion pups as an indirect indicator of maternal diets during gestation. Combining these data with isotope data from potential prey species in a Bayesian mixing model, we generated proportional estimates of dietary consumption for key prey. Our analysis indicated that females in the most westerly metapopulations relied heavily on Atka mackerel and squid, whereas females inhabiting the Gulf of Alaska region had a fairly mixed diet, and the metapopulation of Southeast Alaska showed a strong reliance on forage fish. These results are similar to previous data from scat collections; however, they indicate a possible under-representation of soft-bodied prey (squid) or prey with fragile skeletons (forage fish) from analyses of data from scats. This study supports the utility of stable isotope modeling in predicting diet composition in gestating adult female Steller sea lions during winter, using pup vibrissae.

KEY WORDS: Stable isotopes · Vibrissae · Steller sea lion · Carbon · Nitrogen · Mixing model · Diet composition

INTRODUCTION

Populations of apex predators have experienced dramatic declines and extinctions around the world (Myers & Worm 2005, Prugh et al. 2009, Burton et al. 2011). While persecution by humans is the primary cause of many of these declines (Woodroffe & Ginsberg 1998), causal factors are not apparent in some cases (Hilton et al. 2006), including those of Steller sea lions *Eumetopias jubatus* (National Marine Fisheries Service 2008). Given their position among the highest levels in food webs, alterations to communi-
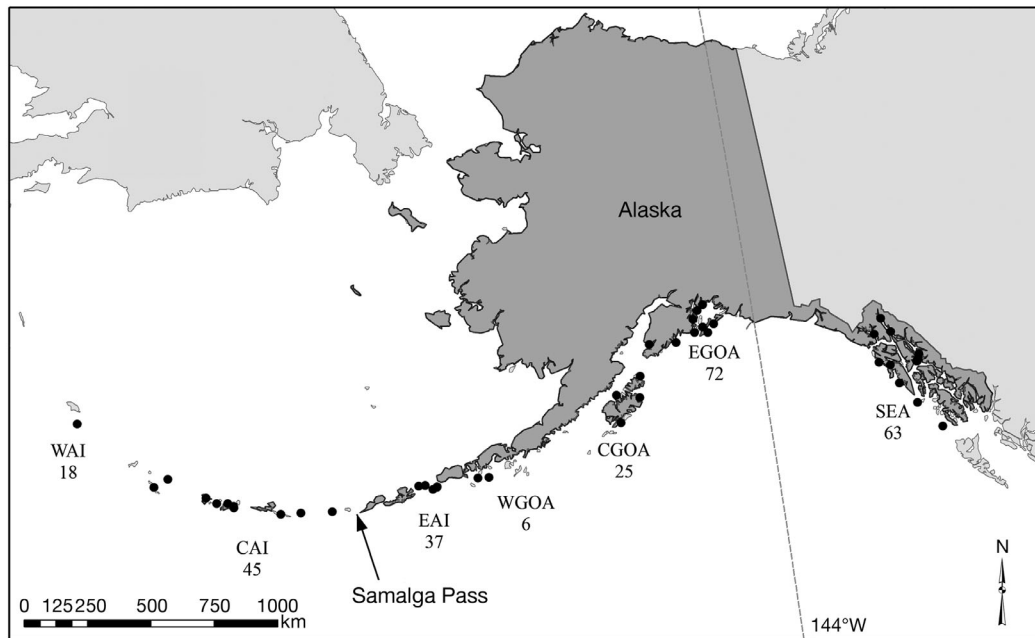
Fig. 1. Distribution of Steller sea lions *Eumetopias jubatus* in the Alaska range, USA. The population is partitioned into 2 distinct population segments (DPS): the western and the eastern DPS, separated at the 144° W meridian. We partitioned the western DPS into 6 metapopulations: Western Aleutians (WAI), Central Aleutians (CAI), Eastern Aleutians (EAI), Western Gulf of Alaska (WGOA), Central Gulf of Alaska (CGOA), and Eastern Gulf of Alaska (EGOA); and the eastern DPS into one meta-population: Southeast Alaska (SEA). Number below each metapopulation label: pup vibrissae sample size; (●) sampling locations

ties at lower trophic levels is a possible cause, and declines in some predator populations have been associated with changes in diet (Hirons et al. 2001, Hilton et al. 2006, Harihar et al. 2011). Knowledge of prey composition in the diets of predator populations is, therefore, necessary for a more complete evaluation of the mechanisms hypothesized to cause changes in demographic rates and conservation status (Arnould et al. 2011, Riemer et al. 2011).

The Steller sea lion (hereafter sea lion) is the largest otariid (eared seal) species and is one of several apex predators in the North Pacific Ocean. Its geographic range extends from the northern coasts of eastern Asia and Japan, eastward along the Aleutian Islands and the coast of mainland Alaska, and southward to Central California (Bickham et al. 1996, Phillips et al. 2011). The portion of the population in the United States is partitioned into 2 distinct population segments (DPS): eastern and western, based on genetic analyses and differences in estimates of population trends (Bickham et al. 1996, Phillips et al. 2011) (Fig. 1). The western DPS is listed as 'endangered' under the US Endangered Species Act (ESA), and long-term data from counts of individuals indicate a decline in abundance of ~80% from estimates made as early as the 1950s (National Marine Fish-

eries Service 2008). Currently, there are variable rates of recovery or continued decline among meta-populations within the western DPS, with the western Aleutian Islands showing the greatest continuing decreases in sea lion numbers (Fritz et al. 2013). The eastern DPS was delisted under the ESA in December 2013 as annual counts indicate a population increase of ~3% yr^{-1} since the 1970s (Pitcher et al. 2007, Trites et al. 2007b).

Several causes of the decline of sea lions in the western DPS have been proposed (National Research Council 2003, Springer et al. 2003, Atkinson et al. 2008, National Marine Fisheries Service 2008), including changes in diet (Merrick et al. 1997, Trites et al. 2007a). Specifically, large-scale changes in climate and oceanographic conditions (i.e. a regime shift) in the mid-1970s led to changes in the spatial distribution and abundance of fish and other prey species in the North Pacific (Pitcher 1981, Hare & Mantua 2000). It has been proposed that the recent diets reflect a greater reliance on species that are less fatty and energy dense, and may prevent sea lions from meeting their energy needs, particularly during specific times of the year (e.g. during gestation and lactation in females) and for life stages with higher energetic demands (e.g. juveniles; Rosen & Trites 2005).

Contemporary diets of sea lions appear to vary longitudinally across western DPS metapopulations. Summer (breeding season) scat samples from metapopulations in the western and central Aleutians indicate high consumption of Atka mackerel *Pleurogrammus monopterygius*, with lower consumption of salmon *Onchorhynchus* spp., cephalopods (e.g. Gonatidae spp. and Octopoda spp.), and walleye pollock (Sinclair & Zeppelin 2002). Beginning in the eastern Aleutians, scat samples indicate increased consumption of walleye pollock, with progressively greater use of walleye pollock and lower use of Atka mackerel in metapopulations to the east (Pitcher 1981, Merrick et al. 1997, Sinclair & Zeppelin 2002, Trites et al. 2007b) (Table 1). The variation in diet across metapopulations is consistent with the spatial variation in prey abundance (Bredesen et al. 2006, Csepp et al. 2011).

While estimates of dietary composition based on scat samples suggest spatial and temporal variation in the diets of sea lions, there are many sources of bias associated with this method (Kurle & Gudmundson 2007, Sinclair et al. 2011). The contributions of larger prey species may be underestimated because hard parts (e.g. bones) from larger prey items tend to be retained in the stomach and may not be present in scats (Sinclair & Zeppelin 2002, Tollit et al. 2009, Sinclair et al. 2011). In addition, soft-bodied prey (e.g. cephalopods and elasmobranchs), prey from which sea lions only consume soft tissue, or prey with fragile skeletons (e.g. small schooling fishes such as Pacific herring), may be absent or difficult to detect in scats (Pitcher 1981, Tollit et al. 2009). The use of

hard parts from scats may also provide a temporally limited view of diet (Kurle & Gudmundson 2007). Spatially and seasonally available prey species (e.g. Pacific herring, eulachon *Thaleichthys pacificus* and salmon) are thought to be important components of sea lion diets when these species are nearshore for spawning or en route to freshwater spawning locations (Womble et al. 2009, Csepp et al. 2011). Therefore, the use of scats may strongly bias estimates of dietary composition toward species that are available at the time of sampling. Finally, it is logistically difficult and expensive to collect scat from remote rookeries and haulouts across the Alaska range, and routine sampling could lead to behavioral disturbance of this endangered species.

Given these potential sources of bias and data limitations, studies that supplement estimates based on scat samples with those derived using other methods are needed (Sinclair et al. 2011). While direct observation of foraging behaviors would be ideal, it is also logistically and financially unfeasible. Examining stomach contents would be an effective method of obtaining a snapshot of dietary consumption; however, the vulnerable and protected status of sea lions makes this an unfavorable option. In contrast, stable isotope analysis of sea lion tissues offers an alternative to estimating dietary composition.

Sea lions are thought to grow their vibrissae continuously without shedding such that multiple years of past dietary history can be investigated for adult and/or subadults (Hirons et al. 2001, Lowther & Goldsworthy 2011, Rea et al. 2015), making this tissue well-suited for stable isotope analysis. This intrinsic record is advantageous in that it provides diet information specific to an individual, compared to scats, where data from a collection of unknown individuals sampled at one location is based on prey frequency of occurrence (FO hereafter). Obtaining vibrissae samples from adult sea lions remains challenging, whereas efforts at capturing pups on terrestrial rookeries have been very successful. Thus, we sought to use vibrissae samples from pups to infer the dietary composition of adult females during gestation. The first step in the development of this stable isotope-based diet assessment using vibrissae records is to corroborate model outcomes against published sea lion diets based on scats. However, this study is limited by the small sample size of vibrissae available from the western Aleutian Islands (the current area of greatest population decline) and the limited stable isotope data currently published for potential sea

Table 1. The subset of prey species included in mixing models for the 7 Steller sea lion *Eumetopias jubatus* metapopulations. Forage species represents a collection of small-bodied fish (eulachon, capelin, sand lance and herring). X: species included in the mixing models for the metapopulation. Metapopulations listed from the westernmost to easternmost are: Western Aleutians (WAI), Central Aleutians (CAI), Eastern Aleutians (EAI), Western Gulf of Alaska (WGOA), Central Gulf of Alaska (CGOA), Eastern Gulf of Alaska (EGOA) and Southeast Alaska (SEA)

Prey species	Metapopulation						
	WAI	CAI	EAI	WGOA	CGOA	EGOA	SEA
Walleye pollock	X	X	X	X	X	X	X
Forage species	X	X	X	X	X	X	X
Arrowtooth flounder				X	X	X	X
Squid	X	X	X				
Pacific cod	X	X	X	X	X	X	X
Rock greenling							
Salmon				X	X	X	X
Atka mackerel	X	X	X				

lion prey across the Alaska range. Therefore, we do not attempt to assess the impact of diet differences on population dynamics among metapopulations, but instead present a test case whereby we generate quantitative diet estimates for late gestation females as inferred from vibrissae collected from their rookery pups.

When a predator consumes all or part of another organism, a portion of the consumed tissue may be excreted or catabolized and used for energy. However, another portion may be digested and assimilated into the tissue of the predator. Consequently, the stable isotope values of a consumer's tissues often reflect the isotope values of its prey, and this relationship can then be used to improve our understanding of the trophic ecology of organisms and the compositions of their diets (Newsome et al. 2010, Ben-David & Flaherty 2012). For viviparous animals, tissue collected from offspring should be informative of the diets of their mothers, particularly if the tissues were grown while the offspring were *in utero* or nursing (York et al. 2008, Habran et al. 2010, Lowther & Goldsworthy 2011, Rea et al. 2015). During these stages, offspring are utilizing their mothers' tissues, and the stable isotope values of the offspring should reflect those of their mothers. We collected vibrissae from pups in 7 metapopulations of sea lions and used the stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values from the vibrissae to estimate the composition of the winter diet of gestating adult female sea lions. We compared these estimates with dietary estimates from studies based on scats to develop a more robust understanding of sea lion diets in the Alaska range, and to establish the utility of stable isotope modeling in predicting diet composition in adult female sea lions, using pup vibrissae.

MATERIALS AND METHODS

Study area

The population of sea lions from which we sampled vibrissae ranged from Agattu Island in the western Aleutian Islands, along the coasts of the Aleutian Islands and mainland Alaska to Hazy Island in Southeast Alaska (Fig. 1). In this study, we treated sea lions of the eastern DPS utilizing rookeries and haulouts in Southeast Alaska (east of 144° W) as a single metapopulation. The western DPS was partitioned into units that we refer to as metapopulations after York et al. (1996). Each metapopulation is a group of individuals that utilizes a specific set of rookeries (where

sea lions breed and raise young in the summer) and haulout sites (terrestrial areas used in winter). Sinclair & Zeppelin (2002) examined scat samples to estimate the dietary composition of sea lions across much of this range and delineated clusters of rookeries and haulout sites with similar diets. We partitioned the population into 7 metapopulations based on the results of their study and by clustering rookeries and haulout sites by geographic proximity (Fig. 1): western Aleutian Islands (WAI), central Aleutian Islands (CAI), eastern Aleutian Islands (EAI), western Gulf of Alaska (WGOA), central Gulf of Alaska (CGOA), eastern Gulf of Alaska (EGOA) and Southeast Alaska (SEA).

Estimating dietary proportions

Stable isotope mixing models are commonly fit to isotopic data from a predator's tissues and the tissues of its putative prey to assess the relative contribution of the prey species to the assimilated diet of the predator (Hopkins & Ferguson 2012). Where data from 2 isotopes (X and Y) have been measured in tissues from a population of predators and the diet of the predator is composed of prey species 1, 2, and 3 (i.e. a '3-source' model), a stable isotope mixing model can be written as follows:

$$\delta X_P = [f_1 \times (\delta X_1 + TEF_1)] + [f_2 \times (\delta X_2 + TEF_2)] + [f_3 \times (\delta X_3 + TEF_3)]$$

$$\delta Y_P = [f_1 \times (\delta Y_1 + TEF_1)] + [f_2 \times (\delta Y_2 + TEF_2)] + [f_3 \times (\delta Y_3 + TEF_3)]$$

$$1 = f_1 + f_2 + f_3 \tag{1}$$

δX_P and δY_P are the values for isotopes X and Y in the tissues of the predator and are described as a linear mixture of the stable isotope values from 3 prey species. The δX and δY to the right of the equal sign are the values for isotopes X and Y in the tissues from prey species 1, 2, and 3. *TEF*s are trophic enrichment or stable isotope discrimination factors, which are reported as Δ^{13}C for carbon and Δ^{15}N for nitrogen. Trophic enrichment occurs as a result of a collection of processes that tend to select against the assimilation of lighter isotopes into a predator's tissues, leading to higher stable isotope values with increasing trophic level. *TEF*s are generally calculated by subtracting the stable isotope value of the prey from that of the consumer in studies of captive animals held on known diets (Hobson et al. 1996). Although the magnitude of trophic enrichment likely varies with the

prey species consumed by a predator (Kurle et al. 2014), species specific values are not available for the mixed diet of these generalist predators. Therefore, we applied a single *TEF* to all prey species. Finally, the subscripted *f*s represent the relative contribution of prey species 1, 2, and 3 to the assimilated diet of the predator and are the parameters in the model (i.e. they are the values that were estimated).

We used the stable isotope mixing model SIAR to derive estimates of dietary composition for adult female sea lions (Parnell et al. 2010). The primary inputs we used were (1) $\delta^{13}C$ and $\delta^{15}N$ values from sea lion pup vibrissae collected from each metapopulation, (2) the mean ($\pm$SD) $\delta^{13}C$ and $\delta^{15}N$ values from potential prey species, and (3) estimates of *TEF*s for each isotope between sea lion vibrissae and their potential prey. The mixing model in SIAR also includes a term for the variance of the residuals for each isotope, σ^2_{13C} and σ^2_{15N}, and these terms are estimated parameters in the model (Parnell et al. 2010).

Collection and preparation of vibrissae and prey stable isotope data

From 1998 to 2011, we collected vibrissae from 266 pups throughout the Alaska range. Sample sizes were highly variable across metapopulations, with <20 pups sampled from the WAI and WGOA and >70 pups sampled from the EGOA (Fig. 1). Pups ranged in age from a few weeks old to nearly 11 mo old.

Growth of sea lion vibrissae occurs at the root, which means that the portion nearest the root represents recent growth while the portion nearest the tip represents the oldest growth (Fig. 2) (Hirons et al. 2001). Each pup vibrissa, therefore, contains a record of diet from early growth *in utero* (near the tip; a reflection of the maternal female's diet during the pup's gestation) through nursing, and potentially
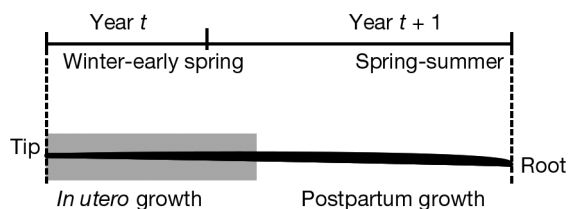

Fig. 2. Vibrissa from a Steller sea lion *Eumetopias jubatus* pup showing regions of *in utero* and postpartum growth, as well as the corresponding seasons of growth. The tip of the vibrissa is grown *in utero* during the winter of year *t* and early spring of year *t* + 1, and the section near the root is grown in the late spring and summer of year *t* + 1

independent feeding by the pup (near the root) (Fig. 2). We cut vibrissae into segments ranging from 0.1 to 4.0 cm in length and measured the $\delta^{13}C$ and $\delta^{15}N$ values in each segment. The variation in segment length was necessary to meet mass requirements for analysis. For the analyses described in this paper, we selected a single segment identified as coming from the *in utero* region of each vibrissa, with the objective of estimating the dietary composition of adult female sea lions in winter. Although sea lions breed in the summer, implantation of the embryo is delayed until September or October. *In utero* growth of pups occurs over the winter and into the subsequent spring. Although vibrissae have been documented on a 2 mo old southern elephant seal fetus (Ling 1977), based on vibrissae of aborted sea lion fetuses and necropsies of pregnant females (Rea pers. obs.), we believe the majority of *in utero* vibrissae growth occurs in the last trimester (i.e. approximately April through June). Thus, selecting a segment of pup vibrissa from the late gestation growth region should provide information about the winter diets of gestating female sea lions.

To identify the portion of the vibrissae that grew while pups were *in utero*, we selected a sample of 20 pups that were 5 mo old or younger when vibrissae were sampled. The total length of the vibrissa collected from each pup was measured, and pup age (in months) was estimated at time of capture based on mean pupping date for each region (Pitcher et al. 2001). We used estimates of monthly growth rates for sea lion pup vibrissae from Rea et al. (2015; 0.87 cm mo^{-1}) to compute the length of postpartum growth, and subtracted that value from the total length of each vibrissa. The resulting value is an estimate of the length of each vibrissa at birth (i.e. the length of *in utero* growth; $\bar{l}$ = 7.79 ± 1.25 cm [SD]). We then selected a segment from this *in utero* region for analysis. To minimize the probability of selecting segments that were grown postpartum, we only selected segments that were a maximum of 4 cm from the tip. The average distance from the tip of a whisker to the midpoint of the chosen segment is 2.4 cm (>88% of segments were <3 cm from the tip).

We analyzed the $\delta^{13}C$ and $\delta^{15}N$ values from the *in utero* vibrissae segments at the Alaska Stable Isotope Facility (University of Alaska Fairbanks) and at the US Geological Survey Stable Isotope Laboratory (Denver, Colorado) after cleaning in an ultrasonic bath using deionized water followed by a 2:1 chloroform:methanol solution. At the Alaska Stable Isotope Facility, samples were measured via combustion using an elemental analyzer (Costech Analytical)

interfaced to an isotope ratio mass spectrometer (DeltaV^{plus}XP CF-IRMS Thermo Fischer LLC) operated in continuous flow mode. Isotopic data are expressed as ratios in delta (δ) notation relative to an international standard (Vienna PeeDee Belemnite for δ^{13}C and atmospheric air for δ^{15}N) in parts per thousand (‰). The mean analytical precision was determined using working laboratory standards (Sigma Chemical: mean δ^{13}C = −15.8‰ and mean δ^{15}N = 7.0‰) and instrument precision was 0.1‰ for δ^{13}C and 0.2‰ for δ^{15}N. At the US Geological Survey Stable Isotope Laboratory, isotopic measurements were made using an elemental analyzer (Carlo Erba NC1500) interfaced to an isotope ratio mass spectrometer (Micromass Optima) operated in continuous flow mode (Fry et al. 1992). Isotopic data were normalized using USGS 40 (−26.24‰ and −4.52‰ for δ^{13}C and δ^{15}N, respectively) and USGS 41 (37.76‰ and 47.57‰ for δ^{13}C and δ^{15}N, respectively) across separate sample runs and instrument precision was <0.2‰.

In addition to the δ^{13}C and δ^{15}N values of tissue from sea lions, estimating dietary composition with stable isotopes requires stable isotope values from a suite of potential prey species. Therefore, we created a database of δ^{13}C and δ^{15}N values from the tissues of many species of fish and other taxa collected throughout the study area from published (Kurle & Worthy 2001, Rand 2007, Kurle et al. 2011), public (Alaska Fisheries Science Center undated, NOAA), and unpublished sources (T. C. Kline & B. Witteveen unpubl. data). These prey samples were collected from 1995 to 2010, thereby overlapping the time period in which the sea lion vibrissae were collected (1998–2011; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m527p261_supp.pdf). We compiled the δ^{13}C and δ^{15}N values for >30 species of fish, 2 species of squid, several crustaceans, and some invertebrates (Table S1 in the Supplement). Kurle et al. (2011) reported variation in the δ^{13}C and δ^{15}N values from prey species collected in the Gulf of Alaska and Bering Sea. Therefore, we assigned a geographic location of either the Bering Sea or the Gulf of Alaska to each sample in the database based on collection location. We assumed that sea lions from the WAI and CAI feed on prey that are isotopically similar to those from the Bering Sea, whereas sea lions from the CGOA, EGOA and SEA feed on prey that are isotopically similar to those from the Gulf of Alaska. The geographic origin of prey for sea lions from the EAI and WGOA was less apparent; therefore, we pooled the stable isotope data from prey across both regions and arrived at an overall estimate of prey δ^{13}C and δ^{15}N values for sea lions in these areas (Table S1). For Pacific cod, we only had one sample from the Gulf of Alaska. Consequently, we added the samples of Pacific cod from the Bering Sea and used these data for mixing models for the metapopulations in the Gulf of Alaska (Table S1).

The δ^{13}C and δ^{15}N values in the prey database were derived from samples of muscle tissue, as well as homogenized tissues from all or large portions of individual prey bodies. We expect δ^{13}C values from these 2 types of tissue samples to differ due to the tendency of muscle to have lower concentrations of lipids. Lipids have lower δ^{13}C values than proteins and carbohydrates, and samples of tissues with high ratios of carbon to nitrogen (C:N > 3.5), as found in lipids, tend to have lower δ^{13}C values (McConnaughey & McRoy 1979, Post et al. 2007). To account for this difference, sampled tissues typically have lipids extracted chemically prior to the measurement of δ^{13}C, or mathematical standardization is often performed for samples that are not lipid-extracted. Our prey database included a mix of non-lipid-extracted samples with C:N ratios >3.5 and we standardized δ^{13}C values by applying the formula of Post et al. (2007); <20% of the prey samples required standardization.

Kurle et al. (2011) also reported seasonal variation in the δ^{13}C and δ^{15}N values among individuals of the same prey species. Because we are interested in the composition of female sea lion diets in winter or early spring when pups are *in utero*, we only used the δ^{13}C and δ^{15}N values from prey samples collected during those time periods when possible (Table S1). Finally, Trites & Calkins (2008) estimated the sizes of individuals consumed by sea lions for several prey species. Because stable isotope values can vary among individual fish and squid of different sizes within a population (Kurle et al. 2011), we used the results of Trites & Calkins (2008) to exclude prey isotope values from prey that were outside the size range most frequently consumed by sea lions.

We used the results of previous studies to identify a subset of prey species from the database that were most likely part of sea lion diets (Table 1). The previous studies included assessments of diets based on identification of hard parts in scats (e.g. Pitcher 1981, Sinclair & Zeppelin 2002, Trites et al. 2007a, Trites & Calkins 2008) and genetic analyses of hard parts and other tissues in scats (Tollit et al. 2009). We also grouped species with similar δ^{13}C and δ^{15}N values or only included one of the species in cases where studies of scats indicated that the species was a much more important component of sea lion diets. For ex-

ample, samples of prey from the Gulf of Alaska indicate that squid are isotopically similar to walleye pollock, which is an important prey species for metapopulations in that region. Therefore, we excluded squid from the mixing models for the WGOA, CGOA, EGOA and SEA metapopulations. The previous studies found little evidence that small-bodied, schooling fishes are significant dietary components for sea lions. However, due to their fragile skeletons, they can be underrepresented in diet studies based on scats (Tollit et al. 2009). We included 4 small forage fish (eulachon, capelin, sand lance *Ammodytes hexapterus* and herring) in the final subset of putative prey species. These species have similar $\delta^{13}C$ and $\delta^{15}N$ values in the database, and we combined them into a single group (forage fish). We did not have isotope data for 4 species or groups of species that appear infrequently in sea lion scat and stomach content samples; these include rock greenling *Hexagrammos lagocephalus*, octopus (Order: Octopoda), Irish lord *Hemilepidotus hemilepidotus*, and skates (Family Rajidae).

Analytical approach

For each prey species or prey group, we computed the mean $\delta^{13}C$ and $\delta^{15}N$ values and standard deviations (Table S1). We derived an estimate of the carbon ($\Delta^{13}C$) and nitrogen ($\Delta^{15}N$) *TEF*s between a female's diet and her pup's vibrissae following Stricker et al. (2015), using a 2-step approach. Stricker et al. (2015) used a controlled feeding experiment to estimate the *TEF*s for sub-adult/adult sea lion vibrissae to diet ($\delta^{13}C = 3.3 \pm 0.3$ SD and $\delta^{15}N = 3.7 \pm 0.3$ SD) and they used free-ranging mother–pup pairs to estimate the difference between a mother's vibrissae and those of her pup ($\delta^{13}C = -0.4$ and $\delta^{15}N = 0.8$). We summed these 2 values to derive estimates of overall *TEF*s from a mother's diet to her pup's vibrissae. Because the mother vibrissae-to-pup vibrissae *TEF*s were not normally distributed (and much smaller), we only used the standard deviation values from the mother's diet-to-vibrissae *TEF*s in our models.

To qualitatively assess the appropriateness of major prey selections and *TEF*s, we plotted the $\delta^{13}C$ and $\delta^{15}N$ values from each sea lion along with the mean (± 1 SD) prey values adjusted for $\Delta^{13}C$ and $\Delta^{15}N$. We examined these plots to determine if a polygon created by connecting the $\delta^{13}C$ and $\delta^{15}N$ values from the set of prey species (i.e. an isotope mixing polygon; Parnell et al. 2010) contained the $\delta^{13}C$ and $\delta^{15}N$ values of the sea lions. Parnell et al. (2010) used simulated datasets to evaluate the performance of SIAR

under a variety of conditions, including data with known violations of assumptions and varying numbers of isotopes and sources. They found that SIAR performed well (95% of the credible intervals contained the true value of parameters in >88% of simulated datasets) under all conditions, although credible interval coverage was poorest when the number of isotopes used in the simulated data was small relative to the number of sources in the mixing model. The maximum number of sources in the models of their simulated data was 5. Consequently, we restricted the number of sources in any mixing model to 5 species or species groups (e.g. forage fish).

For each metapopulation, we ran the model for 3 chains, with 50 000 iterations per chain without the use of informative priors. We specified a burn-in of 10 000 iterations and a thinning rate of 1 in 20 (i.e. we included every 20th iteration in the posterior distribution). Since sea lions feed on prey across a relatively narrow range of trophic levels (i.e. they appear to feed primarily on fish and squid), we assumed no concentration dependence. To assess convergence of each model, we plotted the MCMC chains (after thinning) for each estimated parameter and examined the plots for appropriate mixing among chains (e.g. Fig. S2 in the Supplement).

We report the median of the posterior distributions for f_i (the relative contribution of prey species i) and the variance of the residuals σ^2_{13C} and σ^2_{15N} as estimates of each model's parameters. In addition, we report the 5 and 95% percentiles as lower and upper credible intervals. Correlations between posterior estimates of dietary proportions are reported as Pearson's product-moment correlation coefficients (r). Isotope data were analyzed using R version 3.1.1 (R Core Team 2014) and the SIAR package (Parnell & Jackson 2013). Data ellipses presented in Fig. 3 illustrate the 95% probability ellipse surrounding the $\delta^{13}C$ and $\delta^{15}N$ values for each prey species or species group and were produced using the CAR package (Fox & Weisberg 2011).

RESULTS

Plots of the mean $\delta^{13}C$ and $\delta^{15}N$ values for the sea lions from each of the metapopulations suggested differences in diet between the westernmost metapopulations (WAI and CAI) and the metapopulations to the east (EAI, WGOA, CGOA, and EGOA, and SEA) (Fig. 3). The WAI and CAI metapopulations had lower $\delta^{13}C$ and $\delta^{15}N$ values relative to the remaining metapopulations (Fig. 3).
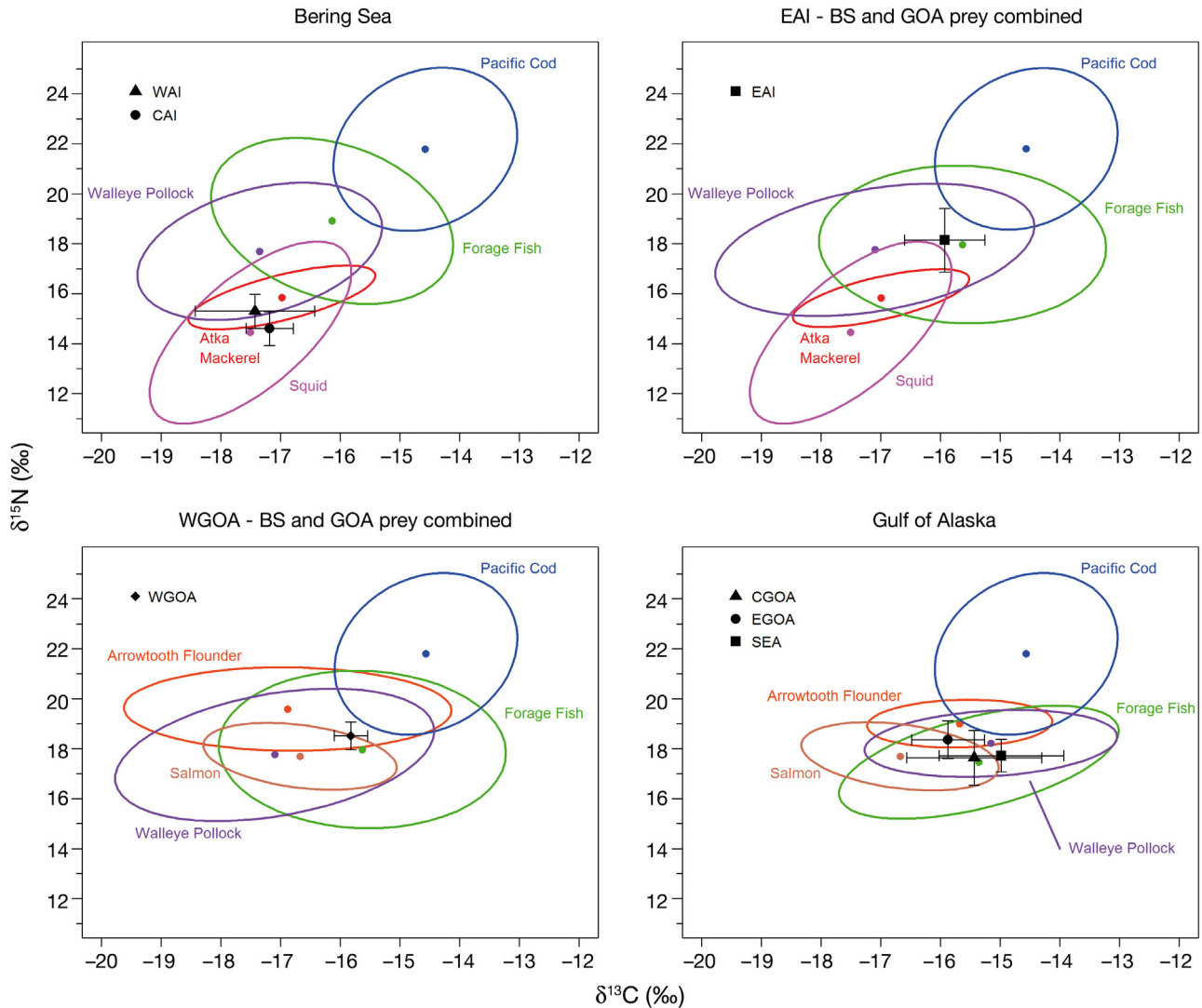
Fig. 3. $\delta^{13}C$ and $\delta^{15}N$ values of Steller sea lions *Eumetopias jubatus* and their potential prey items separated by general collection location (Bering Sea and Gulf of Alaska; EAI and WGOA plots show combinations of Bering Sea and Gulf of Alaska prey data). Black symbols: mean $\delta^{13}C$ and $\delta^{15}N$ values for each sea lion metapopulation (±1 SD). The metapopulations are: Western Aleutians (WAI), Central Aleutians (CAI), Eastern Aleutians (EAI), Western Gulf of Alaska (WGOA), Central Gulf of Alaska (CGOA), Eastern Gulf of Alaska (EGOA) and Southeast Alaska (SEA). Colored data ellipses: stable isotope values of potential prey items, set at a 95% probability level (41 of 42 cod values in the GOA were collected in the Bering Sea; see 'Materials and methods' for details)

Examination of plots of the MCMC chains did not indicate any model convergence problems. The 3 MCMC chains for each parameter mixed well, and estimates from the posterior distributions for each parameter were nearly identical (Fig. S2 in the Supplement).

Estimates of f_i (the relative contribution of prey species to the diet of sea lions) from the SIAR models that were run on the WAI and CAI isotope data indicated that the prey species with the largest contributions to the tissue of sea lions were squid and Atka

mackerel (Table 2, Fig. 4). Estimates for prey consumed by sea lions in the EAI, WGOA, CGOA, and EGOA on the other hand, suggested more diverse diets spread across multiple prey species. This is also reflected in the more central positioning of the stable isotope values from sea lion vibrissae within the prey ellipses as compared to that in the WAI and CAI metapopulations (Fig. 3). Dietary estimates in the EAI were dominated by forage fish and Pacific cod, with additional contributions by squid, Atka mackerel, and very little from walleye pollock. The diets of

Table 2. Estimates of the relative contribution of prey species (f_i) to the assimilated diets of Steller sea lions *Eumetopias jubatus* from 7 metapopulations. LCI(f_i) and UCI(f_i): lower and upper credible intervals, respectively

Metapopulation Prey species	f_i	LCI (f_i)	UCI(f_i)
Southeast Alaska (SEA)			
Arrowtooth	0.03	0.00	0.11
Forage	0.63	0.50	0.75
Pollock	0.27	0.10	0.41
Cod	0.02	0.00	0.07
Salmon	0.03	0.00	0.12
Eastern Gulf of Alaska (EGOA)			
Arrowtooth	0.23	0.03	0.42
Forage	0.15	0.02	0.29
Pollock	0.13	0.01	0.33
Salmon	0.38	0.27	0.52
Cod	0.08	0.01	0.19
Central Gulf of Alaska (CGOA)			
Arrowtooth	0.08	0.01	0.27
Forage	0.42	0.18	0.72
Pollock	0.22	0.02	0.44
Salmon	0.20	0.03	0.38
Cod	0.04	0.00	0.13
Western Gulf of Alaska (WGOA)			
Arrowtooth	0.12	0.01	0.29
Forage	0.24	0.06	0.39
Pollock	0.29	0.15	0.42
Salmon	0.12	0.01	0.30
Cod	0.21	0.07	0.33
Eastern Aleutian Islands (EAI)			
Atka	0.17	0.02	0.37
Forage	0.30	0.08	0.51
Pollock	0.06	0.01	0.18
Cod	0.28	0.16	0.41
Squid	0.15	0.02	0.32
Central Aleutian Islands (CAI)			
Atka	0.35	0.21	0.45
Forage	0.02	0.00	0.07
Pollock	0.01	0.00	0.05
Cod	0.01	0.00	0.04
Squid	0.60	0.51	0.69
Western Aleutian Islands (WAI)			
Atka	0.33	0.10	0.56
Forage	0.04	0.00	0.13
Pollock	0.08	0.01	0.21
Cod	0.02	0.00	0.07
Squid	0.51	0.35	0.66

sea lions from the WGOA were fairly evenly distributed among walleye pollock, forage fish, Pacific cod, salmon and arrowtooth flounder. The model suggested that CGOA sea lion diets were largely made up of forage fish, some walleye pollock and salmon, and very little arrowtooth flounder and Pacific cod. Sea lion diet estimates from the EGOA were dominated by salmon, but also contained arrowtooth

flounder, forage fish, and walleye pollock, with very little Pacific cod. Finally, the model indicated that the largest contributor to SEA sea lion diets were forage fish, with the highest f_i (0.63) among prey. This was followed by walleye pollock and very little contribution by arrowtooth flounder, Pacific cod, and salmon.

DISCUSSION

In agreement with scat-based assessments (Merrick et al. 1997, Sinclair & Zeppelin 2002) and previous stable isotope analyses of blood samples (Kurle & Gudmundson 2007), our models suggested a prominent difference in the dietary compositions of sea lions in the WAI and CAI compared to the EAI and the Gulf of Alaska (WGOA, CGOA, EGOA, and SEA). Although our proportional estimates did not directly correlate with FO-based estimates, a comparison of results offered additional insight into feeding habits. Only 3 studies (Sinclair & Zeppelin 2002, Womble & Sigler 2006, Trites et al. 2007a) reported contemporary diet estimates from scat collected solely in the non-breeding (winter) period and thus provide the most relevant comparison.

Sinclair & Zeppelin (2002) reported a high FO of Atka mackerel collected in the CAI and WAI. While our results attributed a substantial portion of the sea lion diet to Atka mackerel, the models also suggested that squid may have constituted an even greater proportion of the diet in these metapopulations. A strong negative correlation (r ≈ −0.93) between posterior estimates for squid and Atka mackerel proportions (resulting from significant overlap in their δ^{13}C and δ^{15}N values; Fig. 3, Table S1 in the Supplement) suggested that the model was unable to differentiate the relative contributions of these 2 sources. However, the isotopic compositions of vibrissae from sea lions in the CAI and WAI suggested a difference in diets. With the exception of 2 outliers with notably high δ^{13}C values in the WAI, the isotopic compositions of most individuals fell within the overlapping range of stable isotope values from Atka mackerel and squid, hence the large overlap in proportional estimates from our model. Diets of the outliers appear to be comprised of a more even mixture of potential prey items used in our model. The δ^{15}N values from sea lions in the CAI were lower than those in sea lions from the WAI (Welch 2 sample *t*-test: t = −3.6634, df = 31.213, p-value = 0.0009); this may indicate that their diets contained a higher proportion of squid as the δ^{15}N values from squid are lower than those from Atka mackerel. This also likely contri-
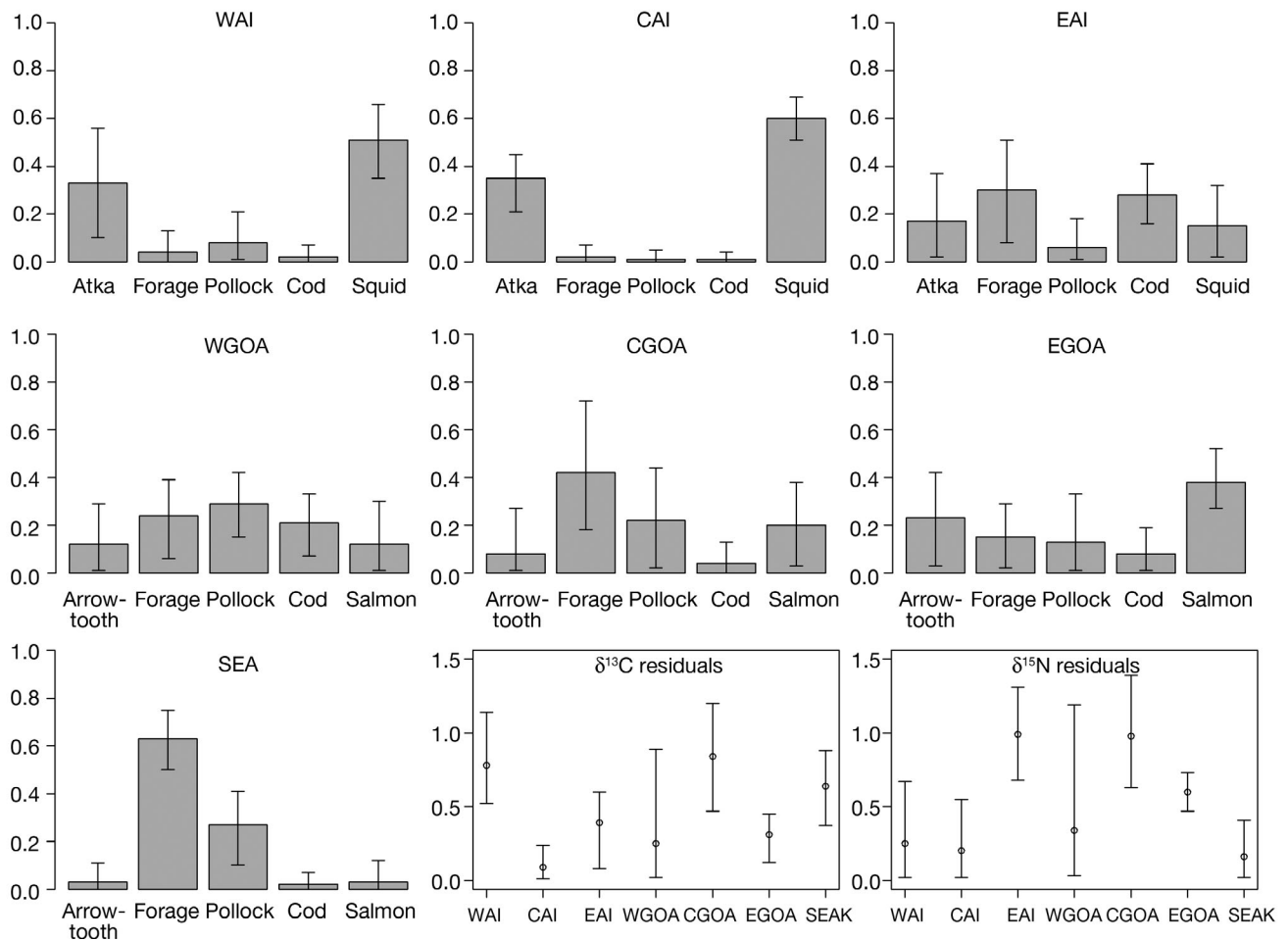
Fig. 4. Proportional estimates of dietary composition for each of the 7 metapopulations of Steller sea lions *Eumetopias jubatus*, as determined in SIAR. Bottom middle and right plots: distribution of variance of the residuals, σ^2_{13C} and σ^2_{15N}. Error bars: upper and lower credible intervals around each estimate

buted to the much smaller variance for these posterior estimates.

The predominance of Atka mackerel and squid in the WAI and CAI sea lion diets compared to the more diverse diets of the EAI–SEA metapopulations may reflect bathymetric changes that occur roughly at Samalga Pass (Fig. 1). East of the pass, the continental shelf may extend >100 km from haulout sites, providing a gentle slope with much seafloor within the diving range of sea lions. West of the pass, the insular shelves are much smaller and steeper, with seafloor depths exceeding sea lion dive range within ~10 km of haulouts. This change in seafloor topography, and associated effects on ocean currents and water chemistry, likely influenced the composition of prey species available to western metapopulations. For example, the range of Atka mackerel extends throughout our study area; however, the center of abundance is located around the

Aleutian Islands (Lowe 2011). Atka mackerel prefer habitat along the shelf edge during the winter season, making accessibility greatest in the WAI and CAI during this season. Additionally, the geographical distribution of squid species is likely mediated by their low tolerance of low salinity waters (Hendrix et al. 1981). Decreased levels of salinity resulting from terrestrial freshwater entering the Alaska Coastal Current persist westward along the southern coast as far as Samalga Pass (Ladd et al. 2005). Thus, squid populations are likely limited in the near-shore foraging grounds east of this pass.

The substantial overlap in credible intervals of proportional dietary estimates for the EAI, WGOA, CGOA and EGOA metapopulations precluded a definitive assignment of dietary composition; however, the models indicated patterns that were not observed in scat studies. For example, in the EAI and CGOA, Sinclair & Zeppelin (2002) found a large

occurrence of walleye pollock and a much lower incidence of forage fish (almost no forage fish species reported in the EAI). Our models suggested a relatively large contribution from forage fish as compared to pollock in both of these metapopulations. However, due to the similar $\delta^{13}C$ and $\delta^{15}N$ values of walleye pollock and forage fish, especially for the CGOA population, these estimates may be more reflective of the relative proximity of the sea lion isotope values to the mean prey isotope values. Thus, the model could not differentiate between the 2 possible sources (each is equally likely), and it defaulted to the prey species with the nearest mean. The correlation between posterior estimates for forage fish and walleye pollock proportions (r = −0.67) in the CGOA diets suggested this situation. In the case of the EAI diets, a correlation coefficient of 0.002 between pollock and forage fish was likely due to the influence of the comparatively large sample size of pollock from the Bering Sea, which biased the distribution toward lower $\delta^{13}C$ values. In this model, pollock was largely ignored and the model struggled to differentiate between combinations of either Atka mackerel or squid (r = −0.73) and forage fish or cod (r = −0.91). In the EGOA, where information on non-breeding diets was unavailable, our model indicated that salmon may have been a significant dietary contributor during the late winter or early spring, which would correspond with salmon movements to inland spawning grounds. Again, this may be the result of a tradeoff between salmon and arrowtooth flounder (r = −0.75) as isotope values were similar.

In contrast to scat studies, our model estimates of forage fish contributions in the SEA greatly outweighed the proportion attributed to walleye pollock. Both Trites et al. (2007a) and Womble & Sigler (2006) found pollock remains in ~90% of scats sampled during the non-breeding season. While Womble & Sigler (2006) reported a similar FO for Pacific herring (the most detected forage fish reported at 91%), Trites et al. (2007a) only found herring in ~36% of scats. Although our model was influenced by the same overlap issues noted above (forage fish and walleye pollock r = −0.81), it also indicated a possible underrepresentation of forage fish in SEA sea lion dietary assessments based on scat sampling. This apparent bias may have been due to the fragile nature of their skeletal material and the resulting difficulty of detection using this method (Pitcher 1981, Tollit et al. 2009).

Our model operated on a number of assumptions, not all of which were fully met in this study. First, the model assumed that all relevant prey items were included. We know we violated this assumption because past studies utilizing scat and stomach contents have documented the presence of many additional prey species. Stable isotope mixing models are not well suited to the inclusion of rare prey items because the emphasis is on mass balance to yield a mean diet mixture. Thus, we parameterized our models using the best available information. We limited our model to 5 species for 2 reasons: (1) isotope data did not exist for many of the potential prey items; and (2) to maintain model performance as demonstrated by Parnell et al. (2010) (i.e. >88% of the 95% credible intervals contain the true value). The model also relied on appropriate *TEF* and food source isotope distributions. Possible fluctuations in *TEF* due to seasonality, diet, and body condition (e.g. see Kurle et al. 2014) as well as geographic and temporal variability in source isotope values (Kurle et al. 2011) that were not adequately characterized in our datasets may have resulted in inaccurate assignments of dietary proportions. Some of these limitations will be resolved through current research measuring the isotopic composition of 10 species of fish and cephalopods collected in the WAI and CAI in the summer and winter months between 2013 and 2014. Furthermore, uncertainties about the phenology of *in utero* vibrissae growth and the mechanisms influencing isotopic incorporation in a developing fetus limit the temporal accuracy of these estimates within the gestation period; this is a potential subject of future research. Nevertheless, the similarity between our estimates and those of previous diet assessments (Sinclair & Zeppelin 2002, Kurle & Gudmundson 2007, Trites et al. 2007a) suggested, at the very least, adequate model performance.

When the differences between scat and stable isotope studies are considered, it is important to remember that the former allow inferences about animal diets based on the portion of diet items (primarily indigestible hard parts) that make it through the digestive tract. In contrast, stable isotope compositions of consumer tissues provide information on assimilated diet. Thus, the digestibility of a particular food source could have significant bearing on whether it is detected in either a scat- or stable isotope-based study. One final consideration is that data from scats on haulout sites (during the winter) are likely from a broader range of sexes and age classes than just gestating adult females (see notes from Sinclair & Zeppelin 2002). Therefore, disagreement between the scat-based studies and this work may have been due to differences in diet across sexes or age classes.

CONCLUSION

The precipitous decline of Steller sea lions in the western DPS has sparked major concern over the health and viability of these metapopulations. With persistent, slow growth in the eastern DPS, some researchers have suggested that differences in resource use may be responsible for the opposing trends in abundance. However, the generalist foraging strategy and marine feeding habitat of sea lions have made it difficult to obtain an accurate description of their dietary habits. Using stable isotope values from vibrissae as an intrinsic biogeochemical marker of past dietary assimilation, this study provided additional evidence that sea lion diets vary between metapopulations along a longitudinal gradient. The substantial overlap in isotope values of potential prey items (likely resulting from their similar trophic levels and feeding habits) makes this a less-than-ideal situation for making rigorous dietary assessments based on this technique alone. However, the similarities between our estimates of dietary composition and those determined by scat sampling were striking, suggesting that stable isotope modeling using pup vibrissae is a viable tool for estimating the diet composition of gestating adult Steller sea lions. By targeting our analysis on the winter diets of gestating females, our results provided valuable insight into the diets of a demographic that directly influence fecundity and population abundance trends. Female nutrition and the resulting body condition are likely important factors influencing reproductive rates associated with the population decline (see Pitcher & Calkins 1981, Pitcher et al. 1998) as poor body condition results in high embryonic and fetal mortality. Determining whether sea lion population trends can be attributed to patterns of dietary consumption could have important consequences for the management and conservation of this species, and the evaluation of current and future fisheries management restrictions; it is therefore a fruitful area of future research.

LITERATURE CITED

Alaska Fisheries Science Center (contact: Kerim Aydin) (undated) Stable isotope collections from the North Pacific 2001–2008. http://s3.nprb.org/datasets/4078b2d5-cecb-4277-8b7b-717eeac21fa2/NPRB.2006.22.Isotopes.xml

Arnould JPY, Cherel Y, Gibbens J, White JG, Littnan CL (2011) Stable isotopes reveal inter-annual and inter-individual variation in the diet of female Australian fur seals. Mar Ecol Prog Ser 422:291–302

Atkinson S, Demaster DP, Calkins DG (2008) Anthropogenic causes of the western Steller sea lion *Eumetopias jubatus* population decline and their threat to recovery. Mammal Rev 38:1–18

Ben-David M, Flaherty EA (2012) Stable isotopes in mammalian research: a beginner's guide. J Mammal 93: 312–328

Bickham JW, Patton JC, Loughlin TR (1996) High variability for control-region sequences in a marine mammal: implications for conservation and biogeography of Steller sea lions (*Eumetopias jubatus*). J Mammal 77:95–108

Bredesen EL, Coombs AP, Trites AW (2006) Relationship between Steller sea lion diets and fish distributions in the eastern North Pacific. In: Trites AW, Atkinson SK, DeMaster DP, Fritz LW, Gelatt TS, Rea LD, Wynne KM (eds) Sea lions of the world. Alaska Sea Grant College Program, Fairbanks, AK, p 131–139

Burton AC, Sam MK, Kpelle DG, Balangtaa C, Buedi EB, Brashares JS (2011) Evaluating persistence and its predictors in a West African carnivore community. Biol Conserv 144:2344–2353

Csepp DJ, Vollenweider JJ, Sigler MF (2011) Seasonal abundance and distribution of pelagic and demersal fishes in Southeastern Alaska. Fish Res 108:307–320

Fox J, Weisberg S (2011) An R companion to applied regression, 2nd edn. Thousand Oaks, Sage, CA. http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Fritz L, Sweeney K, Johnson D, Lynn M, Gelatt T, Gilpatrick J (2013) Aerial and ship-based surveys of Steller sea lions (*Eumetopias jubatus*) conducted in Alaska in June–July 2008 through 2012, and an update on the status and trend of the western distinct population segment in Alaska. US Dept Commer, NOAA Tech Memo NMFS-AFSC-251

Fry B, Brand W, Mersch F (1992). Automated analysis system for coupled δ^{13}C and δ^{15}N measurements. Anal Chem 64:288–291

Habran S, Debier C, Crocker DE, Houser DS, Lepoint G, Bouquegneau J, Das K (2010) Assessment of gestation, lactation, and fasting on stable isotope ratios in northern

elephant seals (*Mirounga angustirostris*). Mar Mamm Sci 26:880–895

Hare SR, Mantua NJ (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog Oceanogr 47: 103–145

Harihar A, Pandav B, Goyal SP (2011) Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. J Appl Ecol 48:806–814

Hendrix J, Hulet W, Greenberg M (1981) Salinity tolerance and the responses to hypoosmotic stress of the bay squid *Lolliguncula brevis*, a euryhaline cephalopod mollusc. Comp Biochem Physiol 69:641–648

Hilton GM, Thompson DR, Sagar PM, Cuthbert RJ, Cherel Y, Bury SJ (2006) A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the rockhopper penguin *Eudyptes chrysocome*. Glob Change Biol 12:611–625

Hirons AC, Schell DM, Finney BP (2001) Temporal records of $\delta^{13}C$ and $\delta^{15}N$ in North Pacific pinnipeds: inferences regarding environmental change and diet. Oecologia 129:591–601

Hobson KA, Schell DM, Renouf D, Noseworthy E (1996) Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. Can J Fish Aquat Sci 53:528–533

Hopkins JB III, Ferguson JM (2012) Estimating the diets of animals using stable isotopes and a comprehensive Bayesian mixing model. PLoS ONE 7:e28478

Kurle CM, Gudmundson CJ (2007) Regional differences in foraging of young-of-the-year Steller sea lions *Eumetopias jubatus* in Alaska: stable carbon and nitrogen isotope ratios in blood. Mar Ecol Prog Ser 342:303–310

Kurle CM, Worthy GAJ (2001) Stable isotope assessment of temporal and geographic differences in feeding ecology of northern fur seals (*Callorhinus ursinus*) and their prey. Oecologia 126:254–265

Kurle CM, Sinclair EH, Edwards AE, Gudmundson CJ (2011) Temporal and spatial variation in the $\delta^{13}C$ and $\delta^{15}N$ values of fish and squid from Alaskan waters. Mar Biol 158:2389–2404

Kurle CM, Koch PL, Tershy BR, Croll DA (2014) The effects of sex, tissue type, and dietary components on stable isotope discrimination factors ($\Delta^{13}C$ and $\Delta^{15}N$) in mammalian omnivores. Isotopes Environ Health Stud 50: 307–321

Ladd C, Hunt GL Jr, Moryd CW, Salo SA, Stabeno PJ (2005) Marine environment of the eastern and central Aleutian Islands. Fish Oceanogr 14(Suppl 1):22–38

Ling JK (1977) Vibrissae of marine mammals. In: Harrison RJ (ed) Functional anatomy of marine mammals, Vol 3. Academic Press, London, p 387–415

Lowe SA (2011) Assessment of the Atka mackerel stock in the Gulf of Alaska. In: North Pacific Fishery Management Council Gulf of Alaska Stock Assessment and Fishery Evaluation Report. NOAA, p 1281–1314

Lowther AD, Goldsworthy SD (2011) Detecting alternate foraging ecotypes in Australian sea lion (*Neophoca cinerea*) colonies using stable isotope analysis. Mar Mamm Sci 27: 567–586

McConnaughey T, McRoy CP (1979) Food-web structure and the fractionation of carbon isotopes in the Bering Sea. Mar Biol 53:257–262

Merrick RL, Chumbley MK, Byrd GV (1997) Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their popula-

tion decline in Alaska: a potential relationship. Can J Fish Aquat Sci 54:1342–1348

Myers RA, Worm B (2005) Extinction, survival or recovery of large predatory fishes. Philos Trans R Soc Lond B Biol Sci 360:13–20

National Marine Fisheries Service (2008) Recovery plan for the Steller sea lion (*Eumetopias jubatus*), revision. National Marine Fisheries Service, Silver Spring, MD

National Research Council (2003) Decline of the Steller sea lion in Alaskan waters: untangling food webs and fishing nets. The National Academies Press, Washington, DC

Newsome SD, Clementz MT, Kock PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. Mar Mamm Sci 26:509–572

Parnell AC, Jackson AL (2013) SIAR: stable isotope analysis in R. R package version 4.2. http://CRAN.R-project.org/package=siar

Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. PLoS ONE 5:e9672

Phillips CD, Gelatt TS, Patton JC, Bickham JW (2011) Phylogeography of Steller sea lions: relationships among climate change, effective population size, and genetic diversity. J Mammal 92:1091–1104

Pitcher KW (1981) Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. Fish Bull 79:467–472

Pitcher KW, Calkins DG (1981) Reproductive biology of Steller sea lions in the Gulf of Alaska. J Mammal 62: 599–605

Pitcher KW, Calkins DG, Pendleton GW (1998) Reproductive performance of female Steller sea lions: an energetics-based reproductive strategy? Can J Zool 76:2075–2083

Pitcher KW, Burkanov VN, Calkins DG, Le Boeuf BJ, Mamaev EG, Merrick RL, Pendleton GW (2001) Spatial and temporal variation in the timing of births of Steller sea lions. J Mammol 82:1047–1053

Pitcher KW, Olesiuk PF, Brown RF, Lowry MS and others (2007) Abundance and distribution of the eastern North Pacific Steller sea lion (*Eumetopias jubatus*) population. Fish Bull 107:102–115

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179–189

Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS, Brashares JS (2009) The rise of the mesopredator. Bioscience 59:779–791

R Core Team (2014). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org/

Rand KM 2007 Longitudinal growth differences in Atka mackerel (*Pleurogrammus monopterygius*): using a bioenergetic model to identify underlying mechanisms. MSc thesis, University of Washington, 50 p

Rea LD, Christ AM, Hayden AB, Stegall VK and others (2015) Age-specific vibrissae growth rates: a tool for determining the timing of ecologically important events in Steller sea lions. Mar Mamm Sci (in press)

Riemer SD, Wright BE, Brown RF (2011) Food habits of Steller sea lions (*Eumetopias jubatus*) off Oregon and Northern California, 1986–2007. Fish Bull 109:369–381

Rosen DAS, Trites AW (2005) Examining the potential for nutritional stress in young Steller sea lions: physiological effects of prey composition. J Comp Physiol B 175: 265–273

Sinclair EH, Zeppelin TK (2002) Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). J Mammal 83:973–990

Sinclair EH, York AE, Antonelis GA (2011) Otolith size and location in digestive tracts of northern fur seals (*Callorhinus ursinus*): implications for dietary interpretations. Mar Mamm Sci 27:421–430

Springer AM, Estes JA, van Vleit GB, Williams TM and others (2003) Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? Proc Natl Acad Sci USA 100:12223–12228

Stricker CA, Christ AM, Wunder MB, Doll AC and others (2015) Carbon and nitrogen isotope discrimination for Steller sea lion (*Eumetopias jubatus*) vibrissae relative to milk and fish/invertebrate diets. Mar Ecol Prog Ser 523: 255–266

Tollit DJ, Schulze AD, Trites AW, Olesiuk PF and others (2009) Development and application of DNA techniques for validating and improving pinniped diet estimates. Ecol Appl 19:889–905

Trites AW, Calkins DG (2008) Diets of mature male and female Steller sea lions (*Eumetopias jubatus*) differ and cannot be used as proxies for each other. Aquat Mamm 34:25–34

Trites AW, Calkins DG, Winship AJ (2007a) Diets of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska, 1993–1999. Fish Bull 105:234–248

Trites AW, Miller AJ, Maschner HDG, Alexander MA and others (2007b) Bottom-up forcing and the decline of Steller sea lions (*Eumetopias jubatus*) in Alaska: assessing the ocean climate hypothesis. Fish Oceanogr 16:46–67

Womble JN, Sigler MF (2006) Seasonal availability of abundant, energy-rich prey influences the abundance and diet of a marine predator, the Steller sea lion *Eumetopias jubatus*. Mar Ecol Prog Ser 325:281–293

Womble JN, Sigler MF, Willson MF (2009) Linking seasonal distribution patterns with prey availability in a central place forager, the Steller sea lion. J Biogeogr 36:439–451

Woodroffe R, Ginsberg JR (1998) Edge effects and the extinction of populations inside protected areas. Science 280:2126–2128

York AE, Merrick RL, Loughlin TR (1996) An analysis of the Steller sea lion metapopulation in Alaska. In: McCullough DR (ed) Metapopulation and wildlife conservation. Island Press, Washington, DC, p 259–292

York AE, Thomason JR, Sinclair EH, Hobson KA (2008) Stable carbon and nitrogen isotope values in teeth of Steller sea lions: age of weaning and the impact of the 1975–1976 regime shift in the North Pacific Ocean. Can J Zool 86:33–44