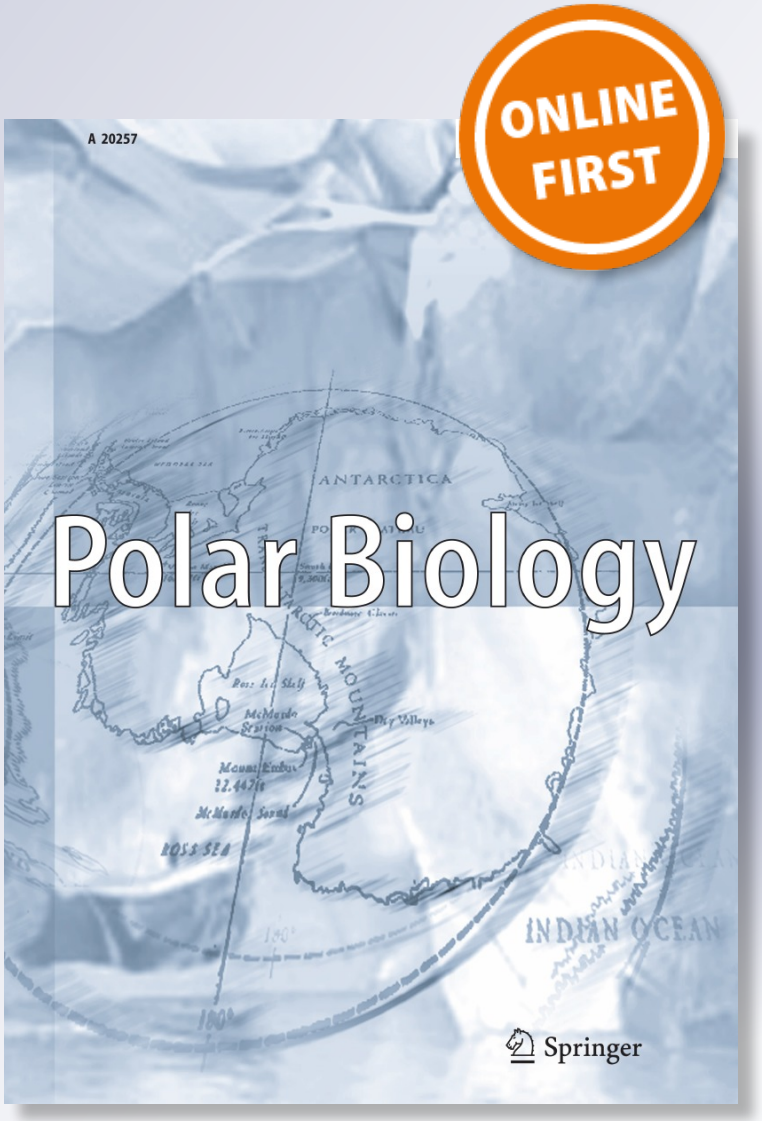
*Proportion of higher trophic-level prey in the diet of Pacific walruses (*Odobenus rosmarus divergens*)*

J. Seymour, L. Horstmann-Dehn & M. J. Wooller

Polar Biology

ISSN 0722-4060

Polar Biol
DOI 10.1007/s00300-014-1492-z



Springer

Polar Biol
DOI 10.1007/s00300-014-1492-z

ORIGINAL PAPER

Proportion of higher trophic-level prey in the diet of Pacific walruses (*Odobenus rosmarus divergens*)

J. Seymour · L. Horstmann-Dehn · M. J. Wooller

Received: 15 August 2013 / Revised: 17 March 2014 / Accepted: 18 March 2014

Abstract During nutritionally stressful situations, Pacific walruses (*Odobenus rosmarus divergens*) may switch from preying on benthic invertebrates to higher trophic-level prey (HTLP) (e.g., pinnipeds and/or seabirds). We applied a Bayesian mixing model to stable isotope (C and N) data from analyses of various tissues (tongue and lumbar muscle, skin, and liver) to quantify the proportional contribution of HTLP to walruses ($n = 293$ individuals). The mode contribution of HTLP to walrus diet was ~22 % (±10 %) based on muscle mixing models, which is consistent with results from contaminant studies of Atlantic walruses (*Odobenus rosmarus rosmarus*), but higher than estimates based on historical stomach content analyses of Pacific walruses. A broader range in the proportion of HTLP (0–60 %) shown by mixing models using stable isotope data from liver and skin of walruses indicated they pursue an opportunistic foraging strategy. Data from the HTLP-consuming walruses were comparable with our stable isotope data of a known "seal-eating" walrus. No significant difference was evident between the estimated contributions of HTLP to the diet of male versus female walruses ($P > 0.01$). This finding suggests that changes in diet base for walruses are not influenced by the sex of the predator.

Keywords Walrus · Stable isotopes · Pinnipeds · Eiders · Mixing model

Electronic supplementary material The online version of this article (doi:10.1007/s00300-014-1492-z) contains supplementary material, which is available to authorized users.

J. Seymour (✉)
School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, P.O. Box 755220, Fairbanks, AK 99775-7220, USA
e-mail: jseymour2@alaska.edu

L. Horstmann-Dehn
School of Fisheries and Ocean Sciences, Institute of Marine Science, University of Alaska Fairbanks, P.O. Box 757220, Fairbanks, AK 99775-7220, USA
e-mail: lara.horstmann@alaska.edu

M. J. Wooller
School of Fisheries and Ocean Sciences, Institute of Marine Science, University of Alaska Fairbanks, P.O. Box 755860, Fairbanks, AK 99775-5860, USA
e-mail: mjwooller@alaska.edu

M. J. Wooller
Alaska Stable Isotope Facility, Water and Environmental Research Center, University of Alaska Fairbanks, P.O. Box 755860, Fairbanks, AK 99775-5860, USA

M. J. Wooller
Alaska Quaternary Center, University of Alaska Fairbanks, P.O. Box 755860, Fairbanks, AK 99775-5860, USA

Introduction

Environmental changes can alter the abundance, distribution, size, digestibility, and energetic content of prey (Barboza et al. 2009). Prey-switching is a common phenomenon of organisms in response to external factors, including declines in prey abundance and increases in predator populations (Bowen et al. 2006; Beaulieu et al. 2009). When preferred prey decline in density or abundance, the energetic cost of foraging and prey handling may increase, and these costs may eventually outweigh the predator's energy gains (Rosen et al. 2007; Barboza et al. 2009). Increased reliance on alternate prey species can mitigate the loss of caloric energy from declines in availability of traditional prey, allowing predators to persist and traditional prey populations to recover.

Published online: 02 April 2014

The changing environment in the Arctic may be prompting Pacific walruses (*Odobenus rosmarus divergens*) toward adopting alternative foraging strategies (Rausch et al. 2007; Jay and Fischbach 2008). Such alterations may take the form of direct changes (e.g., altered diet), or indirect changes in the form of differences in food web dynamics, decreased biomass input to the benthos, and decreases in prey quality (Grebmeier et al. 2006; Grebmeier 2012; Wang et al. 2013). Sea ice, the diving platform that provides walruses with energetically efficient access to benthic invertebrate prey (Fay 1982), has recently displayed unprecedented annual declines (National Snow and Ice Data Center 2012; Stroeve et al. 2012). As the Arctic sea ice retreats to deeper waters, walruses are left without ready access to benthic foraging grounds and may need to adopt alternate strategies to obtain prey, as they are not physiologically adapted to deep diving (Fay 1982). Dietary studies suggest that walruses have increased reliance on high trophic-level prey in recent years, possibly as a result of environmental changes (Seymour et al. 2014).

Walruses are considered benthic specialist predators using highly adapted facial musculature to obtain invertebrate prey from sediments and extract bivalves from their shells, with numerous other benthic invertebrate taxa commonly utilized (Fay 1982; Sheffield and Grebmeier 2009). However, walruses may feed on other available resources, and seal predation or carcass scavenging by walruses are not novel foraging strategies (Fay 1960; Fay et al. 1977; Lowry and Fay 1984; Muir et al. 1995; Mallory et al. 2004; Wolkers et al. 2006; Fox et al. 2010). Fay (1960) suggested that in nutritionally stressful situations or during unfavorable sea ice conditions walruses may prey on seals or birds. Further, increased use of centralized terrestrial haulouts, such as the thousands of walruses hauling out near Point Lay, Alaska in past years (Jay et al. 2012), may lead to localized invertebrate prey depletion and/or create energetically costly increases in travel distances to foraging grounds. This may then result in opportunistic foraging on higher trophic-level prey (HTLP), such as pinnipeds and seabirds. Additionally, recent in situ observations suggest active predation by Pacific walruses (*O. rosmarus divergens*) on spectacled eiders (*Somateria fischeri*, Lovvorn et al. 2010). Marine mammal trophic-level prey shifts may have unforeseen energetic consequences, potentially resulting in declining body condition and fecundity, increased disease susceptibility, decreased offspring survival, and changes in contaminant exposure; all of which can lead to population declines (Kutz et al. 2005; Fischbach et al. 2007; Burek et al. 2008; Garlich-Miller et al. 2011). The degree to which walruses rely on HTLP is not well understood as walrus dietary studies have historically relied on stomach content analysis, a method which is biased toward hard-bodied organisms (Pierce et al. 2004). Walruses preferentially ingest the soft tissues of seals and birds (Lowry and Fay 1984) and stomach content analysis may therefore underestimate the contribution of HTLP to walrus' diet.

Analyses of stable nitrogen isotope ratios ($^{15}N/^{14}N$) can be used to assess trophic position of an organism relative to its prey (Kelly 2000). A stepwise enrichment of 3–5 ‰ per trophic level is generally assumed for marine mammals (Hobson et al. 1996). Stable carbon ($^{13}C/^{12}C$) isotope ratios can be used as an indicator of geographical origin (sourced by primary production as food web base), and little enrichment (0–1 ‰ per trophic level) occurs between prey and consumers in the marine environment (Kelly 2000; Kurle and Worthy 2002). When more than one prey species or prey of different trophic levels are consumed by a predator, isotopic mixing models can be applied to determine the proportional contribution of each source to the predator's diet (Phillips et al. 2005). Depending on fractionation and cellular turnover of different tissues, and the metabolic rate of the predator, stable isotope (SI) signatures can reflect the integrated diet of a consumer from days to years (Hobson et al. 1996; Newsome et al. 2010; Seymour et al. 2014).

We used a Bayesian stable isotope mixing model (SIAR) to examine the proportional contribution of HTLP to the diet of Pacific walruses. While stable isotope analysis (SIA) provides low taxonomic resolution compared to other methods of dietary analysis, such as stomach content and fecal examinations, it provides a tool to assess the importance of prey from different trophic levels to a consumer's diet without biases toward hard-bodied organisms. Assessment of the frequency and consequences of prey-switching by walruses in the Arctic ecosystem would be informative for management of this species, particularly when considering climate change effects on biological diversity and health of the Arctic Ocean.

We hypothesize that walruses rely on HTLP to a larger extent than observed from stomach content analyses. Furthermore, under the suggestion that predation on seals and seabirds is more common among male walruses (Fay 1982; Lowry and Fay 1984), we would expect a greater proportion of HTLP in samples from males. The objectives of this study were to (1) quantify the proportional contributions of HTLP to the diet of Pacific walruses, (2) determine whether multiple tissue types (i.e., lumbar and tongue muscle, skin, and liver) provide homologous SI and Bayesian mixing model results, and (3) investigate whether male and female walruses have different proportional contributions of HTLP in their diet.

Materials and methods

Walrus sample collection

Sources and types of walrus tissues collected and analyzed for this study are presented in Table 1. In 2011, we

Table 1 Sampling year, location, and sample sizes for Pacific walrus (*Odobenus rosmarus divergens*) tissues available for use in this study [sample size (n) = 293 individuals][a]

Location	Source	Type	Date	Available sample (n)			
				Tongue	Muscle	Liver	Skin
St. Lawrence Island	USFWS	Subsistence	2010	73	74	–	–
			2009	49	48	–	5
			1994	–	–	24	–
			1993	–	–	15	–
			1992	–	–	10	–
Chukotka Peninsula	USFWS/Dr. Horstmann-Dehn, UAF	Free-ranging USA/USSR cruise	1991	–	–	10	–
Barrow, Wainwright	NSB-DWM	Subsistence	2009	–	6	–	6
Little Diomede Island	USFWS/Dr. Horstmann-Dehn, UAF	Subsistence	2005	1	–	–	–
			2004	–	2	–	–
			2003	5	7	–	–
			1994	–	–	11	–
			1993	–	–	7	–
			1992	–	–	37	–
Cape Peirce	National Park Service/ Togiak National Wildlife Refuge	Mortality event	2009	5	9	–	–
Bering Sea	USGS	Free-ranging	2009	–	–	–	22
Various, Alaska	ADF&G	Subsistence	2009	3	–	–	–
Various, Alaska	UA Museum of the North	Subsistence	1981–2006	–	32	15	1

[a] Tissues of subsistence-harvested walruses in Barrow and Wainwright were collected under the authority of permit number MA134907-0 issued to T. Hepa, NSB-DWM. Archived walrus tissue samples (liver, muscle, and skin) were provided for analysis by the University of Alaska Museum of the North (Loan # 2010.006.Mamm). All other walrus samples used in this study were obtained under a letter of authorization to Dr. Horstmann-Dehn through the USFWS

obtained muscle and liver from a known "seal-eating" walrus (the stomach contained identifiable parts of two-ringed seals, *Pusa hispida*, Seymour et al. 2014) in collaboration with the NSB-DWM and hunters in Barrow, Alaska.

Tongue and muscle samples were stored in Ziploc™ bags and frozen at −20 °C. Full-thickness blubber samples with attached skin were wrapped and stored in aluminum foil in individual Ziploc™ bags at −80 °C. Archived tissue samples (muscle, skin, and liver) were stored at −80 °C in Cyrovials® (with the exception of Russian-sourced samples, which were stored in trace clean I-CHEM jars with Teflon lining). Further details of walrus tissue sample collection are presented in Seymour et al. (2014).

Walrus stable isotope analysis

All tissues were subsampled using sterile knives and dissection scissors on a clean, stainless steel tray. Samples were transferred to scintillation vials, refrozen at −20 °C, and then freeze-dried for 24–48 h. Following lyophilization, samples were ground into a fine powder using a mortar and pestle. For each sample, 0.2–0.4 mg of tissue was weighed into tin capsules. Walrus samples were analyzed for both stable carbon and nitrogen isotope ratios at the UAF Alaska Stable Isotope Facility using a Costech Elemental Analyzer (ESC 4010) coupled to a Finnigan MAT DeltaPlusXL stable isotope ratio mass spectrometer. Isotope values were expressed relative to atmospheric N_2 (for nitrogen) and Vienna PeeDee Belemnite (VPDB) (for carbon) using the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where differential notation (δX) equals the relative difference between sample and standard stable isotope ratios (R_{sample} and R_{standard}, also notated as $^{15}N/^{14}N$ for nitrogen or $^{13}C/^{12}C$ for carbon). Peptone was analyzed as an internal laboratory working standard every 10 samples. Instrument precision, expressed as 1 standard deviation (SD) calculated from multiple ($n = 46$) analyses of the peptone standard, was ±0.2 ‰ for $\delta^{13}C$ and ±0.1 ‰ for $\delta^{15}N$.

The presence of large amounts of lipid in some tissue types (i.e., skin and liver) can skew the $\delta^{13}C$ value obtained from SIA unless the sample is lipid-extracted or values are mathematically corrected after the SIA (Sweeting et al. 2006). The lean quality of marine mammal muscle, however, allows for the analysis of muscle without lipid extraction (Hoekstra et al. 2002). SIA of lipid-extracted

duplicate skin samples from five walruses were used to develop a lipid normalization equation (below). This equation was then applied to the $\delta^{13}C$ values from the 22 walruses represented solely by skin to compare walrus lipid-corrected skin to muscle/tongue.

$$\delta^{13}C' = -14.58 - 0.07\delta^{13}C$$

The equation is the linear regression ($r = 0.60$) between the $\delta^{13}C$ values of non-lipid-extracted and lipid-extracted skin samples ($n = 5$), where $\delta^{13}C$ is the SI value of the non-lipid-extracted sample and $\delta^{13}C'$ is the lipid-corrected value. Lipid extraction of skin was performed using the method outlined by Bligh and Dyer (1959). Briefly, samples were freeze-dried, then vortexed in 4:1 chloroform–methanol. The supernatant was then removed via pipette and discarded. The extraction process was repeated at least four times or until chloroform–methanol added to the sample remained clear. Samples were then air-dried overnight, freeze-dried for 48 h, and analyzed for stable carbon isotopes.

$\delta^{13}C$ values were corrected for the Suess effect to adjust for the depletion in $\delta^{13}C$ values as a result of increased input of anthropogenically sourced CO_2 into the atmosphere. The corrective equation (below), modified by Misarti et al. (2009), incorporates the maximum annual rate of $\delta^{13}C$ value decrease in the North Pacific (−0.014, from Quay et al. 1992; calculations for Arctic regions are not currently available):

$$\text{Suess effect correction factor} = -0.014^{(b*0.027)}$$

where b is the year of the animal's death subtracted from 1850 (the start of the Industrial Revolution); the constant 0.027 describes the curve for change in the $\delta^{13}C$ values of the world's oceans from 1945 through 1997 as calculated by Gruber et al. (1999).

Prey stable isotope analysis

The HTLP mixing model utilized C and N isotope estimates from three potential prey items. The $\delta^{13}C$ and $\delta^{15}N$ values of *Serripes* spp. soft tissue (a common prey item of walruses, Ray et al. 2006; $n = 12$) were used to represent lower trophic-level prey. The $\delta^{13}C$ and $\delta^{15}N$ values of ringed (*P. hispida*) and bearded seal (*Erignathus barbatus*) muscle, and spectacled eider (*S. fischeri*) muscle were used to represent the contribution of HTLP in the diet of walruses. Prey sample sizes, sources, and SI values are presented in Table 2. While consumption of lipid-rich tissues, such as seal blubber and eider fat, can affect carbon isotope signature of the predator and are consumed by walruses (Lowry and Fay 1984; Seymour et al. 2014), these tissues were excluded from analysis to maintain the simplicity of the model. To examine the possibility that lipid-rich tissue consumption might influence model output, an isotope biplot was generated (Fig. 1).

Table 2 Mean ± SD and range (in parentheses) of bulk stable isotope values of prey items incorporated into the SIAR mixing model

Species	Sample size (n)	Mean $\delta^{15}N \pm$ SD (‰)	Mean $\delta^{13}C \pm$ SD (‰)
Serripes spp. soft tissue[a]	12	9.15 ± 1.5	−18.2 ± 0.6
Mean ice seal muscle[b]	137	17.0 ± 0.8	−18.5 ± 1.4
Ringed seal (*Pusa hispida*) muscle[b]	82	16.0 ± 0.6	−18.5 ± 0.8
Bearded seal (*Erignathus barbatus*) muscle[c]	55	16.8 ± 0.9	−17.1 ± 0.5
Spectacled eider (*Somateria fischeri*) muscle[c]	42	13.5 ± 0.2	−18.8 ± 0.1

[a] Stable isotope values for *Serripes* spp. were provided by Dr. K. Iken, UAF. *Serripes* spp. were collected during the 2004 Bering Sea Integrated Ecosystem Research Project (BEST-BIESP) research cruise

[b] Stable isotope values for ringed (*P. hispida*) and bearded seals (*E. barbatus*) were provided by Dr. L. Horstmann-Dehn, UAF (Dehn et al. 2007). Seal samples were collected from subsistence harvests between 1996 and 2003 in the Bering and Chukchi seas. Both seal species consume benthic and pelagic fishes, crustaceans, and benthic invertebrates, and both occupy a similar trophic level distinct from typical invertebrate walrus prey. We therefore used mean and SD SI values from both species combined in the mixing model

[c] Stable isotope values for lipid-extracted spectacled eider (*S. fischeri*) muscle were provided by Dr. J. Lovvorn, University of Wyoming, Department of Zoology and Physiology. Non-lipid-extracted SI values were unavailable. Eider muscle samples were collected in April 2009 in the wintering area of the species in the Northern Bering Sea

Clam soft tissues were extracted from their shells and analyzed for stable carbon and nitrogen isotope ratios as described above. Mean and SD of non-lipid-extracted bulk stable isotope values were used in the mixing model (lipid-extracted bulk isotope values are not currently available for *Serripes* spp.).

Ice seal tissue samples were processed using the same steps described above for SI analysis of walrus tissue. As with walrus samples, ice seal and spectacled eider (*S. fischeri*) $\delta^{13}C$ values incorporated into the mixing model were not lipid-extracted due to the lean quality of the muscle (Hoekstra et al. 2002; Dehn et al. 2007). Ribbon seals (*Histriophoca fasciata*) were omitted for the purposes of this study as this species has not been documented in walrus stomach contents nor are there any accounts of walruses foraging on this species (Fay 1960; Burns 1970; Sheffield et al. 2001). While spotted seal (*Phoca largha*) remains have occasionally been retrieved from walrus stomachs (Lowry and Fay 1984), this species was excluded from modeling input as SI data were only available for

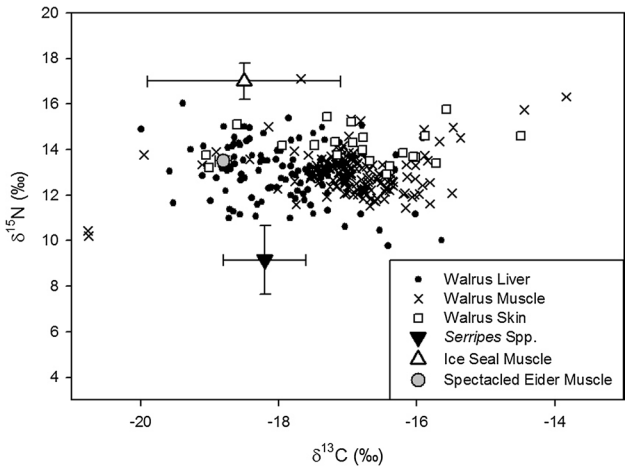


Fig. 1 Scatter plot of Pacific walrus (*Odobenus rosmarus divergens*) stable nitrogen versus stable carbon isotopes (SI) by tissue type and SI means and SDs for representative higher and lower trophic-level walrus prey

young-of-the-year animals whose SI signatures are not necessarily representative of the entire population due to maternal influences (Jenkins et al. 2001). SIAR models were run both with (hereafter EI model) and without (hereafter NE model) stable isotope values for spectacled eiders (*S. fischeri*) to examine the influence of inclusion of eiders in walrus diet on resulting HTLP estimates.

Mixing model

Stable Isotope Analysis in R (SIAR), a Bayesian mixing model within R (version 2.12.2, R Development Core Team 2011), was used to estimate the proportional contribution of prey items (i.e., *Serripes* spp; ice seal, *P. hispida* and *E. barbatus*; spectacled eider, *S. fischeri*) to the diet of walruses. The SIAR program incorporates the stable carbon and nitrogen isotope signatures of predators and representative prey species as well as tissue-specific turnover rates to produce high, low, mean, and mode estimates of the proportion of prey taxa in the diet of an individual predator (Parnell et al. 2010). Following Parnell et al.'s recommendations, mode estimates were used in this study. The model's use of Bayesian statistics allows for incorporation of a greater number of prey sources into the mixing model as well as uncertainty and variation of prey stable isotopes (Parnell et al. 2010). It is ideal to use tissue-specific turnover rates for the predator species; however, for many species, including walruses, these rates are not known (Bond and Diamond 2011). In the absence of this information, we used the turnover rate for ringed seal muscle (2.4 ‰ δ^{15}N, 1.3 ‰ δ^{13}C, Hobson et al. 1996), the closest evolutionary relative to walruses with a known turnover rate.

Statistical analyses

Statistical analyses and visual representations of data were performed in SigmaPlot (version 10.0, Systat Software Inc. 2006). Data failed normality and homogeneity assumptions ($P < 0.05$), and so one-way ANOVAs on ranked data were performed (Iman and Conover 1979), followed by Dunn's multiple comparison tests to assess differences in δ^{13}C and δ^{15}N values among different walrus tissues (i.e., muscle, tongue, skin, and liver) and to examine differences in the mixed model HTLP estimates among walrus tissue types. A Mann–Whitney test was used to assess differences in tissue-specific mixing model outputs between NE and EI models. One-way ANOVA on ranks followed by Dunn's multiple comparison test was also applied to each data set (muscle NE model, muscle EI model, liver NE model, liver EI model) to examine possible differences in δ^{15}N and δ^{13}C values between sexes (skin models were excluded as all skin samples were from female walruses). All statistical analyses were run with $\alpha = 0.05$.

Results

SI signatures of walrus muscle, liver, and skin, and mean SI signatures and standard division of the three representative prey items are presented as a biplot (Fig. 1). Walrus tissues with depleted carbon isotope signatures were assumed to have ingested lipid-rich tissue, which themselves have lower carbon SI signatures (DeNiro and Epstein 1977). Mean, SD, data range, and sample size of δ^{13}C and δ^{15}N values for all walrus tissues are provided in Table 3. These values were compared among walrus muscle, tongue, and lipid-corrected skin from a subset of 28 individuals to determine whether multiple tissues can provide statistically similar isotopic information (Table 4). Liver was not available in combination with the other walrus tissue types, thus no comparison among liver and other tissues from the same individual could be made. Statistical analysis showed no significant difference between δ^{15}N values from walrus muscle, tongue, and lipid-corrected skin ($P > 0.05$, Table 3). A significant difference was found when δ^{13}C values from different walrus tissues were compared ($P < 0.001$) with lipid-corrected skin being more enriched in carbon-13 compared with muscle.

Based on statistical analysis, muscle (lumbar and tongue) data were pooled for use in mixing model analyses as pooling allowed for a greater sample size with respect to model output. If more than one type of walrus tissue was available from the same individual, muscle was used preferentially in the SIAR model because muscle was the most abundant tissue sampled. In the absence of lumbar muscle, the order of preference for other tissue types was

Table 3 Mean ± SD and range (in parentheses) of walrus bulk stable isotope values and proportional contribution of HTLP to walrus (*Odobenus rosmarus divergens*) diet by tissue, including enrichment factors (mean diet-to-tissue isotope fractionation values) (Hobson et al. 1996) and protein half-life turnover rates (skin, Welle 1999; liver, Kurle and Worthy 2002; muscle, Seymour et al. 2014) using both inclusion (EI) and exclusion (NE) of spectacled eiders (*S. fischeri*) in the mixing model (SIAR)

Tissue type	Sample size (*n*)	δ^{15}N diet-tissue isotope fractionation factor (‰)	δ^{13}C diet-tissue isotope fractionation factor (‰)	Protein turnover half-life (days)	Mean δ^{15}N ± SD (‰) (range)	Mean δ^{13}C ± SD (‰) (range)	HTLP (NE model) (range)	HTLP (EI model)	
								Seal (overall range)	Eider
Muscle	154	2.4	1.3	~160[a]	13.0 ± 0.9 (10.0–17.0)	−17.0 ± 0.8 (−14.0 to −20.0)	22.0 ± 10 % (9.0–38.0)	15.0 ± 10 % (2.0–38.0)	9.0 ± 10 %
Tongue	10	n/a	n/a	n/a	13.0 ± 0.5 (12.0–14.0)	−17.0 ± 0.5 (−15.0 to −19.0)	23.0 ± 10 % (13.0–36.0)	16.0 ± 9 % (17.0–37.0)	9.0 ± 10 %
Skin (lipid-corrected)	22	2.3	2.8	~20[a]	14.0 ± 0.7 (13.0–16.0)	−17.0 ± 1.1 (−13.0 to −16.0)	44.0 ± 8 % (31.0–49.0)	61.0 ± 4 % (57.0–64.0)	1.0 ± 3 %
Liver	107	3.1	0.6	~1.9–6.7[a]	13.0 ± 1.2 (10.0–16.0)	−18.0 ± 0.8 (−16.0 to −21.0)	10.0 ± 10 % (1.0–22.0)	5.6 ± 4 % (3.4–20.0)	6.0 ± 10 %

[a] Tissue turnover rates for most walrus (*O. rosmarus divergens*) tissues are currently unknown. Seymour et al. (2014) extrapolated a turnover rate for walrus muscle tissue. To date, Kurle and Worthy (2002) present the only measured turnover rates for pinniped liver (from northern fur seals, *Callorhinus ursinus*). Pinniped skin tissue turnover rates have not been yet been measured. Welle (1999) reported skin tissue turnover rates for humans, which are presented here to provide a rough estimate of pinniped skin turnover rates

tongue muscle, skin, and liver. This order was selected based on turnover rate, with tongue muscle likely having the turnover rate most comparable to lumbar muscle (and statistically similar bulk stable isotope signatures), followed by skin, and then liver. Separate mixing models were generated for walrus liver and skin due to significant differences in their δ^{13}C values compared with muscle.

Higher trophic-level feeding

Mode and SDs of the proportional contributions of HTLP to walrus diet for both the NE and EI models are presented by tissue type in Table 3. Percent HTLP estimates and bulk stable isotope signatures of individual tissue samples are detailed in Appendix A of Supplementary Material. The mode contribution of HTLP when walrus tongue and muscle tissues were combined was 22 ± 10 % for the NE model and 23 ± 10 % when eiders (*S. fischeri*) were considered in the model (EI model). When muscle/tongue and liver mixing model outputs were compared, there was a statistically significant difference ($P < 0.01$) between HTLP estimations, with contribution of HTLP estimated from walrus liver being significantly lower (10 ± 10 %, Table 3). There was a significant difference between lipid-corrected skin HTLP estimates when all possible walrus tissue data were compared (muscle and tongue vs skin) ($P < 0.01$, both models). However, comparisons between the muscle and lipid-extracted skin of the five walruses from which the lipid correction equation was developed, showed no significant difference in HTLP proportions between muscle and skin ($P = 0.20$).

Contribution of HTLP and sex

The sex of the sampled walrus did not significantly impact the proportional contribution of HTLP in either model utilizing walrus muscle ($P > 0.05$, Table 5). Likewise, δ^{15}N values did not vary significantly with sex regardless of tissue type ($P > 0.05$, Table 3). Sex influenced δ^{13}C values in walrus muscle, with males ($n = 46$) having relatively higher values compared with females ($n = 111$, $P < 0.05$, Table 5). No significant difference in δ^{13}C values between males and females was evident from the walrus liver analyses ($P > 0.05$, Table 5).

Discussion

Diet assessments of marine mammals provide a basis for understanding the impacts of environmental change and alterations in prey base on both an individual and population level. Dietary analyses, of marine mammals in particular, can be logistically difficult and are often invasive

Table 4 Tissue comparison (one-way ANOVA on ranks) of SIAR mixing model estimates for proportional contribution of HTLP to the diet of walruses (*Odobenus rosmarus divergens*)

Tissue comparison[a]	Sample size (*n*)	Significant difference in HTLP ($P < 0.05$)
Muscle and tongue	28 (muscle), 11 (tongue)	No ($P = 0.67$)
Muscle and lipid-corrected skin	28 (muscle), 16 (skin)	Yes ($P < 0.001$)
Tongue and lipid-corrected skin	11(tongue), 16 (skin)	Yes ($P < 0.001$)

[a] Liver was not available in combination with other tissue types; thus, no comparison among liver and other tissues from the same individual could be made

(Burns et al. 1998). The ability to assess diet of walruses using bulk stable isotopes in a variety of tissues (especially tissues that can be obtained during minimally invasive biopsy sampling, i.e., skin) is thus extremely valuable. However, caution must be exercised in the choice of tissue type(s). The isotopic information contained in a specific tissue is the result of fractionation factors and cellular turnover (i.e., tissue turnover rates) and the metabolic rate of the predator (Hobson et al. 1996; Newsome et al. 2010). For walruses, different skeletal muscles (tongue and lumbar muscle) from the same individual produce $\delta^{13}C$ and $\delta^{15}N$ values more similar to each other than non-muscle tissue. This is reasonable as metabolic/isotopic turnover rates in different muscles are likely to be closer than turnover rates between skin and muscle or liver and muscle (Hobson et al. 1996; Newsome et al. 2010; Todd et al. 2010). While we initially concluded from comparison of all 293 individuals (with one tissue type representing each animal) that $\delta^{13}C$ values were not homogeneous between muscle and lipid-corrected skin, comparison between the tissue sets of the five individuals (i.e., both skin and muscle samples from each animal) from which our lipid correction equation was developed proved similar ($P = 0.09$). These findings suggest that the $\delta^{13}C$ and $\delta^{15}N$ values of different tissues from the same walrus may provide statistically similar results and that the non-homogeneity observed when our entire sample pool was compared by tissue type could have been the result of comparing different animals with each other (i.e., variation may not be due to comparing skin with muscle, but rather comparing individuals with each other). Such variation among individuals can arise from differences in metabolic rate, which often result from changes in energetic demand associated with migration, reproduction, lactation, growth, and body condition (Barboza et al. 2009; Newsome et al. 2010). Alternately or in addition, variation can be the result of individual dietary preferences and history. It is further possible that the sample size of our pilot study was too small to capture

Table 5 Mean ± SD of walrus (*Odobenus rosmarus divergens*) bulk stable isotope values and proportional contribution of HTLP to diet by tissue and sex using both inclusion (EI) and exclusion (NE) of spectacled eiders (*S. fischeri*) in the mixing model (SIAR)

Sex	Tissue type[a]	Sample size (*n*)	Mean $\delta^{15}N \pm SD$ (‰)	H_0^b	Mean $\delta^{13}C \pm SD$ (‰)	H_0^b	HTLP (NE model)	HTLP (EI model)		H_0^c
								Seal	Eider	
Female	Muscle/tongue	111	13.0 ± 0.6	$P = 0.95$ (NE)	−17.0 ± 0.6	$P = 0.04$ (NE)	21.0 ± 10 %	14.0 ± 10 %	11.0 ± 10 %	$P = 0.57$ (NE)
Male	Muscle/tongue	46	13.0 ± 1.4	$P = 0.18$ (EI)	−17.0 ± 1.2	$P = 0.01$ (EI)	23.0 ± 10 %	19.0 ± 10 %	5.0 ± 10 %	$P = 0.18$ (EI)
Female	Liver	65	13.0 ± 1.1	$P = 0.75$ (NE)	−18.0 ± 0.7	$P = 0.15$ (NE)	10.0 ± 10 %	5.0 ± 4 %	6.0 ± 10 %	$P = 0.87$ (NE)
Male	Liver	25	13.0 ± 1.5	$P = 0.75$ (EI)	−18.0 ± 1.0	$P = 0.14$ (EI)	9.0 ± 10 %	5.0 ± 10 %	6.0 ± 10 %	$P = 0.14$ (EI)

Tongue and lumbar muscle bulk stable isotope data were pooled as no significant differences were found in $\delta^{13}C$ values ($P \geq 0.05$), $\delta^{15}N$ values ($P = 0.61$), and HTLP estimates ($P \geq 0.05$)

[a] Skin samples were excluded from sex-categorical analysis as skin was only available from females

[b] H_0 testing lack of difference in stable isotope signatures between sexes

[c] H_0 testing lack of difference in %HTLP between sexes

significant variation. Additional research comparing SI values of different tissues from a larger sample set and use of captive dietary studies could confirm whether the SI information of different tissues can be directly compared.

Higher trophic-level feeding

The overall proportional contribution of HTLP to walrus diet, as indicated by both the muscle NE and EI Bayesian mixing models, is ~22.0 and 23.0 %, respectively. These proportions are higher than anticipated based on walrus stomach content analyses from the 1980s (~10 %, Lowry and Fay 1984). However, our results support the hypothesis by Rausch et al. (2007) and Lowry and Fay (1984) that predation on seals by walruses has been increasing over the last 40 years. We note, however, that the above historical data come from stomach content analysis and are thus not directly comparable to the results of our mixing models. Furthermore, the proportion of HTLP estimated by our models closely matches the magnitude of HTLP consumption suggested from bioaccumulating contaminant analysis of Atlantic walruses (*O. rosmarus rosmarus*, 25.0 %; 13 of 53 animals, Muir et al. 1995), where predation on seals and birds has been well documented (Muir et al. 1995; Mallory et al. 2004; Fox et al. 2010). Our findings are supported by stomach content and SI analysis of the known seal-eater we examined in 2011, which contained the remains of two-ringed seals as well as quantities of *Mya* spp. siphons (a common benthic bivalve prey of walruses) and displayed a muscle HTLP value of 42 % (Seymour et al. 2014). Further support for opportunistic prey selection comes from the wide range in HTLP values indicated by the liver mixing models (>1–22 %, Table 3), if we assume that walrus liver turnover rate is higher than that of muscle (Tiezsen et al. 1983).

While energetic requirements for Pacific walruses (*O. rosmarus divergens*) are unavailable, Born et al. (2003) estimated that Atlantic walruses (*O. rosmarus rosmarus*) require a gross 896 kJ/kg wet body weight daily. Applied to Pacific walruses (using weights from Fay 1982), an adult male walrus (~1,200 kg) would need 256,800 kJ per day (and a female weighing ~830 kg needs 191,744 kJ per day). We estimated the quantity of lower versus HTLP needed to meet these requirements as follows, using bivalves as a representative lower trophic-level prey and ringed and bearded seals as representative HTLP. Average *Serripes* spp. (values are not available for *Mya* spp.) contain 21 kJ/g dry weight (dw) (Hondolero et al. 2012) and dw represents 61 % of the shell-free wet weight of the animal (Ricciardi and Bourget 1998). At 3.05 g dw/clam (Hondolero et al. 2012), male walruses must consume approximately 12 kg dw of the soft parts of bivalves per day (~4,000 clams) and a female ~9 kg dw per day (~3,000 clams, assuming similar metabolic rates). Ice seal blubber is much more energy dense at 34.5 kJ/dw (Kuhnlein and Soueida 1992). Based on an estimated maximum water content of 17 % for pinniped blubber (measured for harbor seals (*Phoca vitulina*) by Bowen et al. 1992), an adult male walrus would only need to consume ~7.5 kg blubber per day (and females ~6 kg per day). An average adult ringed seal weighs 50–70 kg (Usher and Church 1969), about 40 % is blubber (Rig et al. 1990); thus, an adult walrus would only require ~1/3 of an adult ringed seal per day to meet caloric requirements. Fewer animals would be needed if bearded seals were consumed, which weigh 200–250 kg, with similar % blubber mass (Reeves et al. 1992). Ultimately, relatively fewer and/or shorter successful foraging trips would be required daily if blubber constitutes a regular or semi-regular portion of the walrus diet compared to solely relying on benthic invertebrates. However, consumption of uncommon or novel prey items is often associated with increased energy expenditures related to prey capture, and mechanical and chemical digestion (Barboza et al. 2009). Whether predation on HTLP offers a more efficient net energy gain remains unknown, as the energy expenditure associated with walruses capturing and processing seals or seabirds has not been determined. Furthermore, benthic-pelagic uncoupling in the Arctic and sub-Arctic marine environments (Grebmeier et al. 2006) could influence reliance on HTLP by walruses and perceived potential benefits of "seal-eating." Documented alterations in Arctic and sub-Arctic prey populations in response to environmental variables are not yet fully understood (Grebmeier 2012), but decreases in prey quantity, quality, and distribution all can affect the energetic costs of foraging. Comparisons of %HTLP in walrus diets across different years suggest that the factors influencing walrus' reliance on HTLP are more complex than merely trends in sea ice extent (Seymour et al. 2014).

We note that while walruses occasionally forage on spectacled eiders (*S. fischeri*) and other seabirds, the values generated by the muscle EI mixing model (6–8 % of the diet, Table 3) in this study should be considered objectively, given historical analyses of walrus stomach contents rarely found evidence of seabird consumption (Fay 1982; Fay et al. 1990). Recent studies do suggest seabirds may now comprise a larger portion of the walrus diet (Mallory et al. 2004; Fox et al. 2010). It is also plausible that SIAR's ability to delegate proportions of prey is reduced in the EI models as the $\delta^{15}N$ values of eiders (14.0 ± 0.2 ‰) falls approximately midway between that of ice seals (17.0 ± 0.8 ‰) and *Serripes* spp. (9.0 ± 1.5 ‰), and $\delta^{13}C$ values of all three representative prey species are within 1 SD of each other (−19.0 ± 0.1, −19.0 ± 1.4, and −18.0 ± 0.6 ‰, respectively), making both HTLP isotopically similar to each other and difficult to apportion for

the model. The distribution of walrus tissue SI values was negatively correlated between the ice seal (*P. hispida* and *E. barbatus*) and spectacled eider (*S. fischeri*) SI signatures (Fig. 1), sometimes an indication that the SIAR model will be unable to differentiate between two prey sources (Inger et al. 2010).

As an alternative or in combination with consumption of ice seals and seabirds, it is conceivable that prey with similarly high $\delta^{15}N$ values (such as scavenging benthic crustaceans or predatory gastropods) may contribute to HTLP estimates found in this study. Scavenging crustaceans from the Chukchi Sea region display relatively high $\delta^{15}N$ values (16.0 ‰ for *Sclerocrangon boreas*, Dehn et al. 2007, 16.0 ‰ for *Buccinum* spp., 14.0 ‰ for *Neptunea heros*, Feder et al. 2011) and have been identified in walrus stomach contents (Sheffield and Grebmeier 2009), and the presence of these invertebrates likely reflects variations in regional habitat use.

Contrary to our hypothesis that males constitute the portion of the population preying on HTLP, our models indicate that prevalence of HTLP in both males and females is apparently similar. This finding is divergent from Alaskan local ecological knowledge (LEK) asserting that rogue male walruses are the only individuals to prey on seals and are obligatory seal-eaters (Fay 1960; personal communication with St. Lawrence Island subsistence hunters and the Eskimo Walrus Commission). However, the lack of a significant difference in HTLP consumption between males and females is consistent with previous stomach content analyses (Fay et al. 1977; Fay 1982; Lowry and Fay 1984; Sheffield et al. 2001). Based on female and calf stomach content analyses, Fay et al. (1977) further hypothesized that females might preferentially seek out calorically dense seal blubber to offset the high energetic costs of reproduction. It is likely that obligate seal-eaters exist within the Pacific walrus stock, as Alaskan hunters report seal-eating walruses as morphologically distinct (i.e., yellow tusks and greasy appearance, Fay 1960). The one walrus harvested near Barrow that had recently eaten seals (Seymour et al. 2014) did not exhibit the morphologically distinct characteristics of an obligate seal predator (per. comm. G. Krafsur, NSB-DWM). Preliminary SIA of a whisker from this animal showed fluctuations in its reliance on HTLP over time (Seymour et al. 2014) and indicates that this walrus had consumed seals in the past.

The significant difference in $\delta^{13}C$ values of males versus females shown by the muscle SIA implies that sexes utilize different habitat for foraging. While a preliminary explanation might be differences in ingested % lipid (lipids typically have relatively lower $\delta^{13}C$ values compared to proteins, DeNiro and Epstein 1977), this difference is unlikely the result of variation in tissue lipids as C:N ratios were comparable ($P = 0.62$). C:N ratios would be higher for individuals with lower carbon-13 SI signatures if the difference in carbon-13 was the result of consuming comparatively lipid-rich prey. It is known that $\delta^{13}C$ values vary geographically (Crawford et al. 2008). Seasonal changes in $^{13}C/^{12}C$ are driven by fluctuations in primary productivity (Hobson et al. 1996). However, as extrapolated turnover estimates show walrus muscle $\delta^{13}C$ values to be integrated over roughly 2 years (Seymour et al. 2014), it is unlikely that differences in the $\delta^{13}C$ values are seasonally driven. Walruses occupy geographically distinct regions throughout the year based on semi-sexually segregated migrations (Fay 1982; Garlich-Miller et al. 2011). Additionally, elemental tooth composition suggests that the Pacific walrus (*O. rosmarus divergens*) population may be comprised of several stocks (Jay et al. 2008). The opportunistic nature of the sample collection in our study precludes us from analyzing regional influence on diet as our samples are not regionally representative of the walrus range.

Sexual partitioning of foraging areas (proximity to shore or geographical region) would result in varying intensities of impact on walrus population segments from environmentally induced changes in prey base. Female walruses with dependent calves may be most adversely affected by declines in prey quantity or quality due to their higher energetic demands (Barboza et al. 2009). Ongoing monitoring efforts have revealed declines in fecundity and lipid stores among female walruses (Garlich-Miller et al. 2006) and increased calf abandonment related to poor sea ice conditions (Metcalf and Robards 2008). The magnitude of these impacts will be dependent on whether the severity and extent of alterations in the prey base exceeds walrus dietary plasticity (Barboza et al. 2009). Alternately, sexual-segregated migrations may be declining as more mixed-sex walrus herds have been observed in recent summer months in the Chukchi Sea, an area historically used by females and calves (Garlich-Miller et al. 2011). This trend may explain the lack of differences in reliance on HTLP and absence of a difference in $\delta^{13}C$ values between sexes when liver models are analyzed, assuming that liver turnover rates are higher than muscle and represent a time period of approximately 3 months as described above (Table 5). A continued increase in mixed-sex herds could disperse localized climate change impacts more evenly among the population. The ability to understand the impacts of climate change on walrus population will be dependent on unraveling correlations among climate, consumer, and prey.

The wide range in mode proportional dietary contribution of HTLP (average of $\sim 22 \pm 10$ %, range of 2–38 % based on muscle) suggests that most walruses feed opportunistically on seals or HTLP with similar $\delta^{15}N$

signatures when and where available. Seasonal reliance on HTLP would be reflected by more consistent %HTLP across most samples, as the majority of samples were collected during the spring subsistence harvest, April–May. This finding is supported by the fluctuating $\delta^{15}N$ signature found along the length of a whisker from a known seal-eating walrus (Seymour et al. 2014). The proportional contribution of HTLP found in our analyses is higher than the historical 10 %, suggesting climate impacts on walrus foraging brought on by changes in sea ice quality and extent or more complex environmental and ecological variables. However, historical analyses based on gut content may underestimate the past significance of ice seals and sea birds as walrus prey.

Ultimately, walruses appear to pursue a more generalist approach to foraging than traditionally believed. If so, the dietary breadth and plasticity of the species will serve to mitigate effects from abrupt and/or short-term changes in the prey base. To accurately establish the proportional contribution associated with specific prey species, a combination of methods, including bulk and compound-specific SIA, fatty acid signature analysis, and stomach content analysis combined with developing techniques in fecal DNA analysis, will prove most useful. Continued monitoring of diet through a combination of these analytical methods will provide the best understanding of trends in walrus foraging and a better foundation for assessing population-level dietary consequences of climate change.

Acknowledgments We thank the Eskimo Walrus Commission and the Alaskan coastal communities of Barrow, Diomede, Gambell, Savoonga, and Wainwright for providing walrus tissue samples from their subsistence harvests. We gratefully acknowledge the Alaska Department of Fish and Game, U.S. Fish and Wildlife Service, and North Slope Borough Department of Wildlife Management for logistical coordination, particularly B. Adams, A. Bryan, J. Garlich-Miller, C. George, C. Hanns, G. Krafsur, C. Nayakik, Sr., L. Quakenbush, T. Sformo, and J. Snyder. We further thank U.S. Geological Survey, particularly A. Fischbach and C. Jay, for providing skin samples from their ongoing biopsy program, the University of Alaska Museum of the North for providing archived walrus tissue (Loan # 2010.006.Mamm, samples UAM 24069, 36307, 36308, 36312, 36313, 36317, 36322, 36324, 36325, 36339, 36342, 36349, 36355, 49575, 54001, 60205, 60206, 60211, 60212, 60346, 60352, 60383, 60410, 83321, 85027, 85036, 85043, 88474, 88491, 88493, 88514, 97916, 97932, 98208, 98209, 98210, 99576, 99579, 99594, 99595, 99599, 99600, 99951, 99972), and Togiak National Wildlife Refuge for sharing samples from the 2009 Cape Peirce mortality event, K. Iken for providing *Serripes* spp. stable isotope values, J. Lovvorn for providing spectacled eider stable isotope values, and to the staff of the Alaska Stable Isotope Facility, particularly T. Howe and N. Haubenstock. Funding was provided by University of Alaska Fairbanks through Dr. Horstmann-Dehn, the North Pacific Research Board (Project #901), and the Cooperative Institute for Alaska Research (GC 10-04). K. Seymour provided thoughtful insight on early drafts of this manuscript. The content of this manuscript was greatly improved by the comments of S. Atkinson, C. Rosa, G. Sheffield, P. Barboza, D. Piepenburg, and three anonymous reviewers.

References

Barboza PS, Parker KL, Hume ID (2009) Integrative wildlife nutrition. Springer, Berlin

Beaulieu M, Dervaux A, Thierry AM, Lazin D, Le Maho Y, Ropert-Coudert Y, Spée M, Raclot T, Ancel A (2009) When sea-ice clock is ahead of Adélie penguins' clock. Funct Ecol 24:93–102

Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. Can J Biochem Physiol 37(8):911–917

Bond AL, Diamond AW (2011) Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. Ecol Appl 21:1017–1023

Born EW, Rysgaard S, Ehlmé G, Sejr M, Acquarone M, Levermann N (2003) Underwater observations of foraging free-living Atlantic walruses (*Odobenus rosmarus rosmarus*) and estimates of their food consumption. Polar Biol 26:348–357

Bowen WD, Oftedal OT, Boness DJ (1992) Mass and energy transfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). Physiol Zool 65(4):844–866

Bowen WD, Beck CA, Iverson SJ, Austin D, McMillan JI (2006) Top predators in marine ecosystems. Cambridge University Press, Cambridge

Burek KA, Gulland FMD, O'Hara TM (2008) Effects of climate change on Arctic marine mammal health. Ecol Appl 18:S126–S134

Burns JJ (1970) Remarks on the distribution and natural history of pagophilic pinnipeds in the Bering and Chukchi Seas. J Mammal 51(3):445–454

Burns JM, Trumble SJ, Castellini MA, Testa JW (1998) The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. Polar Biol 19:272–282

Crawford K, MacDonald RA, Bearhop S (2008) Applications of stable isotope techniques to the ecology of mammals. Mamm Rev 38(1):87–107

Dehn L-A, Sheffield G, Follman EH, Duffy LK, Thomas DL, O'Hara TM (2007) Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. Polar Biol 30(2):167–181

Deniro MJ, Epstein S (1977) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42:495–506

Fay FH (1960) Carnivorous walruses and some arctic zoonoses. Arctic 13:111–122

Fay FH (1982) Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. N Am Fauna 74:1–279

Fay FH, Feder H, Stoker SW (1977) An estimation of the impact of the Pacific walrus population on its food resources in the Bering Sea. U.S. Marine Mammal Commission, MMC-75/06, Washington, DC

Fay FH, Sease JL, Merrick RL (1990) Predation on a ringed seal, *Phoca hispida*, and a black guillemot, *Cepphus grylle*, by a Pacific walrus, *Odobenus rosmarus divergens*. Mar Mamm Sci 6(3):348–350

Feder HM, Iken K, Blanchard AL, Jewett SC, Schonberg S (2011) Benthic food web structure in the southeastern Chukchi Sea: an assessment using $\delta^{13}C$ and $\delta^{15}N$ analyses. Polar Biol 34(4):521–532

Fischbach AS, Amstrup SC, Douglas DC (2007) Landward and eastward shift of Alaskan polar bear denning associated with recent sea ice changes. Polar Biol 30(11):1395–1405

Fox AD, Fox GF, Liaklev A, Gerhardsson N (2010) Predation of flightless pink-footed geese (*Anser brachyrhynchus*) by Atlantic walruses (*Odobenus rosmarus rosmarus*) in southern Edgeøya, Svalbard. Polar Res 29:455–457

Garlich-Miller J, Quakenbush LT, Bromaghin JF (2006) Trends in age structure and productivity of Pacific walruses harvested in

the Bering Strait region of Alaska, 1952–2002. Mar Mamm Sci 22(4):880–896

Garlich-Miller J, MacCracken JG, Snyder J, Meehan R, Myers M, Wilder JM, Lance E, Matz A (2011) Status review of the Pacific walrus (*Odobenus rosmarus divergens*) report. U.S. Fish and Wildlife Service Report, pp 2–52

Grebmeier JM (2012) Shifting patterns of life in the Pacific Arctic and Sub-Arctic seas. Annu Rev Mar Sci 4:63–78

Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack EC, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt SL (2006) A major ecosystem shift in the northern Bering Sea. Science 311(5766):1461–1464

Gruber N, Keeling CD, Bacastow RB, Guenther PR, Lueker TJ, Wahlen M, Meijer HA, Mook WG, Stocker TF (1999) Spatiotemporal patterns of carbon-13 in the global surface oceans and the oceanic Suess effect. Glob Biogeochem Cycles 13(2):307–335

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(4):611–625

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

Hoekstra PF, Dehn LA, George JC, Solomon KR, Muir DC, O'Hara TM (2002) Trophic ecology of bowhead whales (*Balaena mysticetus*) compared with that of other arctic marine biota as interpreted from carbon-, nitrogen-, and sulfur-isotope signatures. Can J Zool 80:223–231

Hondolero D, Bluhm BA, Iken K (2012) Caloric content of dominant benthic species from the northern Bering and Chukchi Seas: historical comparisons and the effects of preservation. Polar Biol 35(4):637–644

Iman RL, Conover WJ (1979) The use of the rank transform in regression. Technometrics 21:499–509

Inger R, Jackson A, Parnell A, Bearhop S (2010) SIAR v4 (Stable Isotope Analysis in R): an ecologist's guide. http://www.tcd.ie/Zoology/research/research/theoretical/siar/SIAR_For_Ecologists.pdf

Jay CV, Fischbach AS (2008) Pacific walrus response to Arctic sea ice losses. U.S. Geological Survey Fact Sheet 2008-3041

Jay CV, Outridge PM, Garlich-Miller JL (2008) Indication of two Pacific walrus stocks from whole tooth elemental analysis. Polar Biol 31(8):933–943

Jay CV, Fischbach AS, Kochnev AA (2012) Walrus areas of use in the Chukchi Sea during sparse sea ice cover. Mar Ecol Prog Ser 468:1–13

Jenkins SG, Partridge ST, Stephenson TR, Farley SD, Robbins CT (2001) Nitrogen and carbon isotope fractionation between mothers, neonates, and nursing offspring. Oecologia 129:336–341

Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can J Zool 78(1):1–27

Kuhnlein HV, Soueida R (1992) Use and nutrient composition of traditional Baffin Inuit foods. J Food Compos Anal 5(2):112–126

Kurle CM, Worthy GAJ (2002) Stable nitrogen and carbon isotope ratios in multiple tissues of the northern fur seal *Callorhinus ursinus*: implications for dietary and migratory reconstructions. Mar Ecol Prog Ser 236:289–300

Kutz SJ, Hoberg EP, Polley L, Jenkins EJ (2005) Global warming is changing the dynamics of Arctic host-parasite systems. Proc Biol Sci 272(1581):2571–2576

Liedberg P, Garlich-Miller J, Meehan R (2009) Walrus mortality event Cape Peirce, Alaska-October 2009. News Release

Lovvorn JR, Wilson JJ, McKay D, Bump JK, Cooper LW, Grebmeier JM (2010) Walruses attack spectacled eiders wintering in pack ice of the Bering Sea. Arctic 63(1):53–56

Lowry LF, Fay FH (1984) Seal eating by walruses in the Bering and Chukchi Seas. Polar Biol 3:11–18

Mallory ML, Woo K, Gaston AJ, Davies WE, Mineau P (2004) Walrus (*Odobenus rosmarus*) predation on adult thick-billed murres (*Uria lomvia*) at Coats Island, Nunavut, Canada. Polar Res 23(1):111–114

Metcalf V, Robards M (2008) Sustaining a healthy human–walrus relationship in a dynamic environment: challenges for comanagement. Ecol Appl 18(2 Suppl):S148–S156

Misarti N, Finney B, Maschner H, Wooller MJ (2009) Changes in northeast Pacific marine ecosystems over the last 4500 years: evidence from stable isotope analysis of bone collagen from archeological middens. Holocene 19(8):1139–1151

Muir DCG, Segstro MD, Hobson KA, Ford CA, Stewart REA, Olpinski S (1995) Can seal eating explain elevated levels of PCBs and organochlorine pesticides in walrus blubber from eastern Hudson Bay (Canada)? Environ Pollut 90(3):335–348

National Snow and Ice Data Center (2012) A summer storm in the Arctic. Arctic Sea Ice News & Analysis. http://nsidc.org/arcticseaicenews/2012/08/a-summer-storm-in-the-arctic/. Accessed 14 Aug 2012

Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. Mar Mamm Sci 26(3):509–572

Oftedal OT (2000) Use of maternal reserves as a lactation strategy in large mammals. Proc Nutr Soc 59(1):99–106

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

Phillips DL, Newsome SD, Gregg JW (2005) Combining sources in stable isotope mixing models. Oecologia 44:520–527

Pierce GJ, Santos MB, Learmonth JA, Mente E, Stowasser G (2004) Methods for dietary studies on marine mammals. The Mediterranean science commission: investigating the roles of cetaceans in marine ecosystems. Venice, Italy. 28–31 Jan 2004

Quay PD, Tilbrook B, Wong CS (1992) Oceanic uptake of fossil fuel CO_2: carbon-13 evidence. Science 256(5053):74–79

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org/

Rausch R, George JC, Brower HK (2007) Effect of climatic warming on the Pacific walrus and potential modification of its helminth fauna. J Parasitol 93(5):1247–1251

Ray GC, McCormick-Ray J, Berg P, Epstein HE (2006) Pacific walrus: benthic bioturbator of Beringia. J Exp Mar Biol Ecol 330(1):403–419

Reeves R, Stewart B, Leatherwood S (1992) The Sierra Club handbook of seals and sirenians. Sierra Club Books, San Francisco

Ricciardi A, Bourget E (1998) Weight-to-weight conversion factors for marine benthic macroinvertebrates. Mar Ecol Prog Ser 163:245–251

Rosen DAS, Winship AJ, Hoopes LA (2007) Thermal and digestive constraints to foraging behaviour in marine mammals. Philos Trans R Soc Lond B Biol Sci 362(1487):2151–2168

Ryg M, Lydersen C, Markussen NH, Smith TG, Øritsland NA (1990) Estimating the blubber content of phocid seals. Can J Fish Aquat Sci 47(6):1223–1227

Seymour J, Horstmann-Dehn L, Wooller MJ (2014) Inter-annual variability in the proportional contribution of higher trophic levels to the diet of Pacific walruses. Polar Biol. doi:10.1007/s00300-014-1460-7

Sheffield G, Grebmeier JM (2009) Pacific walrus (*Odobenus rosmarus divergens*): differential prey digestion and diet. Mar Mamm Sci 25(4):761–777

Sheffield G, Fay FH, Feder H, Kelly BP (2001) Laboratory digestion of prey and interpretation of walrus stomach contents. Mar Mamm Sci 17(2):310–330

Sponheimer M, Robinson TF, Cerling TE, Tegland L, Roeder BL, Ayliffe L, Dearing MD, Ehleringer JR (2006) Turnover of stable carbon isotopes in the muscle, liver, and breath CO_2 of alpacas (*Lama pacos*). Rapid Commun Mass Spectrom 20(9):1395–1399

Stroeve JC, Serreze MC, Holland MM, Kay JE, Malanik J, Barrett AP (2012) The Arctic's rapidly shrinking sea ice cover: a research synthesis. Clim Change 110:1005–1027

Sweeting CJ, Polunin NVC, Jennings S (2006) Effects of chemical lipid extraction and arithmetic lipid correction on stable isotope ratios of fish tissues. Rapid Commun Mass Spectrom 20(1):595–601

TE Sub Systems Inc. and Sax Software (2006) SigmaPlot for Windows®. Version 10.0. Germany

Tiezsen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. Oecologia 57(1–2):32–37

Todd SK, Holm B, Rosen DAS, Tollit DJ (2010) Stable isotope signal homogeneity and differences between and within pinniped muscle and skin. Mar Mamm Sci 26(1):176–185

Usher PJ, Church M (1969) On the relationship of weight, length, and girth of the ringed seal (*Pusa hispida*) of the Canadian Arctic. Arctic 22(2):120–129

Wang SW, Budge SM, Gradinger RR, Iken K, Wooller MJ (2013) Fatty acid and stable isotope characteristics of sea ice and pelagic particulate matter in the Bering Sea: tools for estimating sea ice algal contribution to Arctic food web production. Oecologia. doi:10.1007/s00442-013-2832-3

Welle S (1999) Human protein metabolism. Springer, Berlin

Wolkers H, van Bavel B, Ericson I, Skoglund E, Kovacs KM, Lydersen C (2006) Congener-specific accumulation and patterns of chlorinated and brominated contaminants in adult male walruses from Svalbard, Norway: indications for individual-specific prey selection. Sci Total Environ 370(1):70–79