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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Resource partitioning between Pacific walruses and bearded seals in the Alaska Arctic and sub-Arctic

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Abstract Climate-mediated changes in the phenology of Arctic sea ice and primary production may alter benthic food webs that sustain populations of Pacific walruses (*Odobenus rosmarus divergens*) and bearded seals (*Erignathus barbatus*). Interspecific resource competition could place an additional strain on ice-associated marine mammals already facing loss of sea ice habitat. Using fatty acid (FA) profiles, FA trophic markers, and FA stable carbon isotope analyses, we found that walruses and bearded seals partitioned food resources in 2009–2011. Interspecific differences in FA profiles were largely driven by variation in non-methylene FAs, which are markers of benthic invertebrate prey taxa, indicating varying consumption of specific benthic prey. We used Bayesian multi-source FA stable isotope mixing models to estimate the proportional contributions of particulate organic matter (POM) from sympagic (ice algal), pelagic, and benthic sources to these apex predators. Proportional contributions of FAs to walruses and bearded seals from benthic POM sources were high [44 (17–67)% and 62 (38–83)%, respectively] relative to other sources of POM. Walruses also obtained considerable contributions of FAs from pelagic POM sources [51 (32–73)%]. Comparison of $\delta^{13}C$ values of algal FAs from walruses and bearded seals to those from benthic prey from different feeding groups from the Chukchi and Bering seas revealed that different trophic pathways sustained walruses and bearded seals. Our findings suggest that (1) resource partitioning may mitigate interspecific competition, and (2) climate change impacts on Arctic food webs may elicit species-specific responses in these high trophic level consumers.

Keywords Fatty acid · Benthic trophic ecology · Compound-specific · Stable isotope analysis · Climate change · *Odobenus rosmarus divergens* · *Erignathus barbatus*

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Introduction

Extensive sea ice decline and a temporal shift in seasonal Arctic sea ice retreat have important implications for ice-associated marine mammals, such as Pacific walruses (*Odobenus rosmarus divergens*) and bearded seals (*Erignathus barbatus*). Both species primarily rely on benthic food resources in the Bering, Chukchi, and western Beaufort seas (Lowry et al. 1980; Fay 1982; Fay et al. 1984). Whereas bearded seals are less reliant on sea ice for foraging (Quakenbush et al. 2011), walruses use ice that is available to them within areas of foraging to rest between dives

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(Burns and Frost 1979; Fay 1982; Jay et al. 2010). Projected changes in the sea ice environment may affect access to and availability of benthic prey, potentially affecting resource partitioning between walruses and bearded seals.

Changes in sea ice extent and timing of retreat may impact walruses' access to benthic prey. A reduction in the geographic extent of walrus foraging areas could, in turn, influence resource partitioning between walruses and bearded seals. Walruses utilize ice floes to access food resources on the Beringian shelf (Burns and Frost 1979; Ray et al. 2006). However, in recent years, sea ice retreated north of the shelf break, limiting its availability in shallow areas of the Chukchi Sea where walruses typically forage and rest (Jay et al. 2012). As a result, walruses came ashore to terrestrial haul-out locations in large aggregations that have exceeded 30,000 animals (Jay and Fischbach 2008; Monson et al. 2013). Although walruses have used terrestrial haul-out sites on the Russian coast for several decades (Kryukova et al. 2014), the presence of large walrus herds on the northwest coast of Alaska has been less common, though not unprecedented (Collins 1940). This behavior may have consequences for foraging energetics and prey selection (Costa 1991; Rosen et al. 2007; Noren et al. 2012). At haul-out sites, walruses become central place foragers, a strategy that could risk rapid depletion of local benthic food resources (e.g., Costa 1991; Womble et al. 2009). In years of low ice cover in the Chukchi Sea relative to historical records, walruses foraged more frequently in nearshore locations, some characterized by low caloric density (Jay et al. 2012; Wilt et al. 2014), and swam longer distances to access benthic hotspots or ice floes (Jay et al. 2012). When access to preferred feeding grounds is limited, walruses may also opportunistically consume prey that they encounter in the pelagic realm (e.g., seabirds or seals—Collins 1940; Lowry and Fay 1984; Donaldson et al. 1995). These changes in foraging behavior could increase competition among walruses and between walruses and bearded seals in these coastal locations and decrease competition elsewhere.

Sea ice conditions also influence algal production within the sea ice, under the ice, and in open water, as well as deposition on the seafloor, thus affecting the composition and distribution of benthic invertebrate communities (e.g., Grebmeier et al. 2006a; Arrigo 2013; Boetius et al. 2013). Changes in sea ice and algal phenology appear to differ in direction and magnitude between the Bering and Chukchi seas, however (e.g., Brown and Arrigo 2012), so the overall impact on benthic prey availability in foraging areas used by walruses and bearded seals remains unclear.

In the Bering Sea, sea ice cover varies among years, fluctuating between "warm" and "cold" periods. In cold years (e.g., 2007–2014), sea ice melts in spring and releases sea ice particulate organic matter (sympagic or ice—i-POM), which sinks to the benthos ungrazed, where it provides an important food source to benthic fauna (Grebmeier et al. 2006a). Ice melt also releases nutrients needed to seed a phytoplankton bloom in the water column at the ice edge (pelagic—p-POM) (Sakshaug and Skjoldal 1989; Perrette et al. 2011). I-POM and p-POM deposited on the sediment can also be oxidized by sediment microbial communities, creating a unique phytodetrital POM source (benthic—b-POM) that is available to benthic fauna (Oxtoby et al. 2016). In contrast, warm years (e.g., 2001–2005) are characterized by earlier ice retreat (Stabeno et al. 2012), which may have implications for trophic pathways, including those that sustain benthic biomass. In the Bering Sea, earlier ice melt may result in intensified wind mixing, which prevents stratification and delays the development of pelagic blooms (Hunt et al. 2002, 2008, 2011). When a pelagic bloom occurs later in the season, pelagic algal grazers are abundant and consume the p-POM before it sinks to the benthos (Walsh and McRoy 1986; Huntley and Lopez 1992). An ecological shift in the Bering Sea in which more production is partitioned to the pelagic realm and benthic prey resources concurrently decline (Grebmeier et al. 2006b; Grebmeier 2012) could result in increased competition among benthic-feeding marine mammals, such as walruses and bearded seals.

In the adjacent Chukchi Sea, however, recent observations of under-ice pelagic blooms suggest that export of production to the benthos may continue and possibly increase in this region, given the potentially high biomass and large spatial extent of these early season phytoplankton blooms (Arrigo et al. 2012, 2014; Lowry et al. 2014). Additional research is necessary to anticipate shifts in algal production and deposition in the Bering and Chukchi Seas, and any resulting changes in the benthic ecosystem under future climate scenarios.

Bearded seals and walruses have coexisted for thousands of years on the Beringian shelf, sharing food resources and foraging grounds in the Bering and Chukchi seas (Repenning 1976; Lowry et al. 1980; Harington 2008). Current understanding of ice-associated pinniped feeding ecologies is based on traditional ecological knowledge (TEK) (e.g., Noongwook et al. 2007; Huntington and Quakenbush 2013), stomach content analysis (e.g., Sheffield and Grebmeier 2009; Crawford et al. 2015), stable isotope analyses (e.g., Dehn et al. 2007; Seymour et al. 2014a, b), and, occasionally, direct observations of foraging (e.g., Donaldson et al. 1995; Lovvorn et al. 2010). Fatty acids (FAs) have been used to infer dietary niche separation between walruses and bearded seals (Budge et al. 2007) and to examine possible competition over benthic resources (Cooper et al. 2009; Wang et al. 2015b). More recently, compound-specific stable isotope analysis (CSIA) of FAs has been used as a tool to estimate proportional contributions of algal

FA sources with unique chemical signatures (e.g., i-POM, p-POM, and b-POM) to ice seals (Wang et al. 2016) and to benthic invertebrates (Oxtoby et al. 2016) to describe trophic connectivity in Arctic and sub-Arctic marine food webs (e.g., Budge et al. 2008; Graham et al. 2014; Wang et al. 2015a). When combined with FA analyses, CSIA of FAs can constrain proportional contributions of unique POM sources (i-POM, p-POM, and b-POM) to the diets of higher trophic level consumers.

In this study, we used a multi-proxy analytical approach (FA trophic markers, profiles, and CSIA of FAs), which provided several lines of evidence from which to interpret variation in the diets and trophic pathways that sustain walruses and bearded seals. Our main objectives were to: (1) describe the degree of dietary overlap between walruses and bearded seals, (2) estimate the proportional contributions of sympagic (i-POM), pelagic (p-POM), and benthic (b-POM) production sources to each species using previously published data (Wang et al. 2014, 2015a; Oxtoby et al. 2016), and (3) interpret differences in diet and trophic pathways between walruses and bearded seals by relating the stable carbon isotope composition of their algal FAs to those from benthic invertebrate prey from distinct feeding groups in the Chukchi Sea (this study) and previously published data from the Bering Sea (Oxtoby et al. 2016).

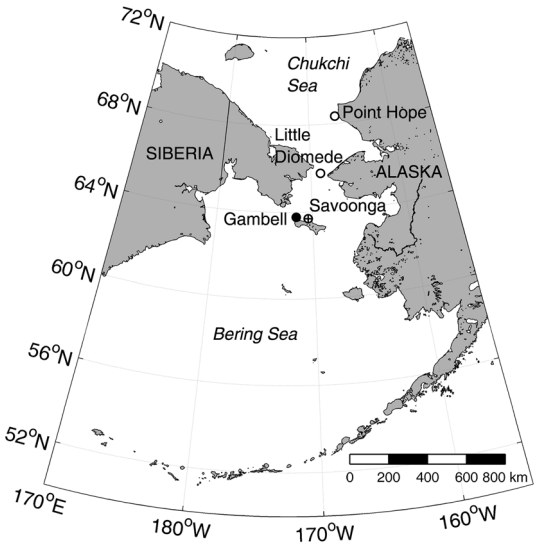

Fig. 1 Locations of Alaskan communities where Pacific walruses (*filled circle*), bearded seals (*open circle*), or both (*circle with cross*) were harvested in 2009–2011. Information on specimens and analyses is provided in Table 1

Materials and methods

Sample acquisition

Walrus specimens were opportunistically sampled during spring/summer subsistence harvests in 2009 ($n = 4$), 2010 ($n = 44$), and 2011 ($n = 9$) near the communities of Gambell and Savoonga on St. Lawrence Island, Alaska (Fig. 1; Table 1). Alaskan Native subsistence hunters provided samples for scientific research in collaboration with the U.S. Fish and Wildlife Service (USFWS), U.S. Geological Survey, the Eskimo Walrus Commission, and the North Slope Borough Department of Wildlife Management. Bearded seals, which were analyzed as part of another study (Wang et al. 2016), were collected in 2009 ($n = 10$) and 2010 ($n = 20$) in cooperation with Alaskan Native subsistence hunters from the communities of Savoonga, Little Diomede, and Point Hope (Fig. 1; Table 1) and the Alaska Department of Fish and Game (ADF&G) Arctic Marine Mammal Program. Bearded seal specimens were processed and analyzed using the same protocols and methodologies as described for walruses (additional information concerning bearded seal specimens is described in Wang et al. (2016)).

Subsistence hunters recorded information about individual walruses harvested, including sex, stomach contents, lactation status, presence of a calf, and body condition of the animals. Estimated ages of walruses were obtained by sectioning teeth to determine the number of growth layer groups in cementum, which correspond to the age of the animal (Mansfield and Fisher 1960) (Matson's Laboratory, Montana, USA). All animals (walruses and bearded seals) included in this study were >4 years of age based on tooth age estimates or hunters' evaluations of morphological and reproductive characteristics of the animals. Blubber samples from muscle to skin were taken from the trunk of the body immediately after death. Due to air temperatures below freezing, samples froze on site and were shipped frozen to UAF, where they were immediately wrapped in aluminum foil, and sealed in plastic bags for storage at −80 °C.

Benthic invertebrate specimens ($n = 160$ from seven taxa) were collected at 14 stations on the Chukchi Sea shelf in August and September 2012 during the Russian–American Long-term Census of the Arctic (RUSALCA), the Chukchi Sea Offshore Monitoring In Drilling Area (COMIDA), and the Arctic Ecosystem Integrated Survey (Arctic EIS) research expeditions. Samples were collected using bottom trawls or van Veen grabs at depths ranging from 34 to 58 m. Benthic prey consisted of an omnivore (the snow crab *Chionoecetes opilio*), a subsurface deposit-feeder (the bivalve *Nuculana radiata*), and suspension/surface deposit-feeders (the bivalves *Liocyma fluctuosa*, *Serripes groenlandica*, *Astarte* spp., *Macoma* spp., and *Ennucula tenuis*). Invertebrate samples were frozen at −20 °C and then freeze-dried in a Virtis Freeze Dryer

Table 1 Sample sizes of Pacific walruses and bearded seals analyzed for fatty acid composition and stable carbon isotope values of fatty acids ($\delta^{13}C_{FA}$)

	Pacific walrus		Bearded seal		
	M	F	M	F	U
FA composition					
2009	4	0	3	5	2
2010	8	11	5	15	0
$\delta^{13}C_{FA}$					
2009	4	0	3	5	2
2010	8	28	5	15	0
2011	1	8	0	0	0

See Fig. 1 for harvest locations

M males, *F* females, *U* unknown sex

(model 52; The Virtis Company, NY, USA) while on board the ship.

Sample preparation and lipid extraction

In preparation for lipid extraction, walrus blubber samples were placed on a sterile glass cutting board, and a sterile knife was used to trim the outermost layer of blubber away to expose inner blubber layers. A longitudinal sample from the exposed muscle to the skin layer (full blubber depth) was removed and weighed (~1 g). Wet weights and dry weights were taken for invertebrate specimens (Mettler 200 analytical balance Greifensee, Switzerland). Invertebrate samples were then homogenized and stored in crimp top vials at −80 °C prior to lipid extraction.

Lipids from full-depth blubber samples were solvent extracted using a modified Folch procedure in a ratio of 8:4:3 of chloroform, methanol, and deionized water (Folch 1957; Budge et al. 2006). Invertebrate samples from the Chukchi Sea, which were collected and analyzed as part of a separate research initiative, were lipid extracted using an accelerated solvent extraction (ASE) system (Dionex ASE 200, CA, USA). Approximately 0.5 g hydromatrix (Dionex, CA, USA) was combined with a subsample of 0.5 g homogenized freeze-dried tissue sample. An 11 ml stainless steel thimble was assembled with two cellulose filters and a thin layer of sand before the hydromatrix and tissue mixture were added. An additional cellulose filter was placed at the top before it was loaded into an ASE system. Dichloromethane (DCM, Fisher Thermo-scientific, Fair Lawn, NJ, USA) with butylated hydroxytoluene (BHT; Sigma Chemical, St. Louis, MO, USA) was added at 100 mg/L to prevent lipid oxidation. The extraction occurred at 85 °C under 1500 psi nitrogen with two static cycles of 5 min each. Fatty acid methyl esters (FAME) for all samples were prepared from lipid extracts using an acidic transesterification procedure according to Budge et al. (2006).

FA analysis and compound-specific stable isotope analysis of FAs

Relative proportions of individual FAs from blubber samples were measured using a Perkin Elmer Autosystem II gas chromatograph (GC) (Perkin Elmer, Boston, MA, USA) with a flame ionization detector (FID) containing a 30 m 0.25 mm i.d. column coated with 50% cyanopropyl polysiloxane (0.25 mm film thickness; J&W DB-23; Folsom, CA, USA). Samples (1 μL of FAME in hexane) were injected in splitless mode and analyzed according to a temperature program detailed in Budge et al. (2006). Each sample was analyzed in duplicate and FA proportions were averaged. FA identities were determined by cross referencing retention times with those from an in house standard (menhaden oil) containing FAs previously identified using GC mass spectrometry (MS) (Thermo Finnigan Polaris Q; Bremen, Germany).

FAs from invertebrate samples were analyzed for their relative concentrations by adding an internal standard (23:0 at 1 mg/20 mg lipid) prior to methylation. Esterified lipid samples were dried (TurboVap) and FAMEs re-suspended in hexane to 20 mg/ml. The FAs 16:1n-7 and 20:5n-3 were identified by comparing peak retention times in gas chromatography (GC-FID, model 6850, Agilent Technologies, Wilmington, DE) to a known FA standard (Supelco, 189-19). The Supelco 189-19 standard was used to create a calibration curve from 0.1 to 1.0 mg for quantification of 16:1n-7 and 20:5n-3. Calibration curves for both FAs were extended utilizing FAME standards (Sigma-Aldrich, Saint Louis, MO, USA) to reach concentrations of 5 mg/ml to encompass the concentration range found in samples. FA areas were corrected using Ackman response factors (Ackman and Sipos 1964), because they vary slightly for different FAs due to the interaction of FAs with the GC flame ionization detector (FID). The Ackman response factor is the recorded areas of the calibration curve divided by the 18:0 area values. The FA 18:0 was used as a baseline reference for Ackman response factors, because it elutes in the middle of the run for most marine samples (Ackman and Sipos 1964). Corrected FA areas were then related back to the area of the internal standard.

$\delta^{13}C$ values of individual FAME from walrus blubber and benthic invertebrate tissues were analyzed at the Alaska Stable Isotope Facility (ASIF) using a GC (Thermo Scientific Trace GC Ultra) linked to an isotope ratio mass spectrometer (IRMS—Thermo Finnigan Delta V) through a combustion interface (IsoLink; http://www.isolink.com). The GC column, temperature program, and mode of injection were the same as for the GC-FID analyses used for

blubber and invertebrate samples. 1 μL of FAME in hexane was injected at a sample concentration of FAME adjusted to generate a voltage of 500–3000 mV for 20:5n-3. We used a FAME standard consisting of 16:0 and 18:0 (Nu-Chek Prep, Inc.; Elysian MN), which we injected throughout sample runs to track analytical error ($n = 20$ injections), which was <0.1‰ and <0.2‰, respectively (expressed as 1 SD of 16:0 and 18:0).

Stable carbon isotope ratios of FAs in a sample are described using the conventional delta (δ) notation in parts per thousand (‰) and are expressed as follows: $\delta^{13}C = [(^{13}C/^{12}C_{standard}/^{13}C/^{12}C_{sample}) - 1] \times 1000$, where the standard is the international reference material Vienna Pee Dee Belemnite (VPDB). We analyzed a standard mixture containing eight calibrated *n*-alkanoic acid esters (Mixture F8, Indiana University Stable Isotope Reference Materials), where r^2 of the known versus expected correlation was >0.99, to calibrate $\delta^{13}C$ values of individual FAs. Expected $\delta^{13}C$ values for FAME from the standard mixture ranged from -23.24 ± 0.01‰ to -30.92 ± 0.02‰. We also corrected $\delta^{13}C_{FA}$ values to account for carbon added during transesterification using the following equation (Eq. 1):

$$\delta^{13}C_{FA} = [(n+1)(\delta^{13}C_{FAME}) - (\delta^{13}C_{methanol})]/n \quad (1)$$

where $\delta^{13}C_{FA}$ is the adjusted value of the FA of interest, n is the number of its carbon atoms, $\delta^{13}C_{FAME}$ is the calibrated value of the FAME, and $\delta^{13}C_{methanol}$ is the stable isotope composition of the carbon contributed by the methanol (Abrajano et al. 1994). $\delta^{13}C_{methanol}$ ($\delta^{13}C_{methanol} = -49$‰) was calculated by subtracting the $\delta^{13}C$ value of esterified 16:0 and 18:0 standards from the corresponding $\delta^{13}C$ values of their free FAs (Wang et al. 2014, 2015a).

FAs are expressed using the nomenclature A:Bn-X, where A indicates the number of carbon atoms, B the number of double bonds, and X the position of the double bond closest to the terminal methyl group of a FA. Non-methylene interrupted (NMI) dienoic and trienoic FAs are distinguished from methylene interrupted FAs by the symbol Δ (e.g., 20:2Δ5,11) and double bond positions are given relative to the carboxylic acid functionality. *Iso*- and *anteiso*-methyl branched FAs are further identified by lowercase italicized letters (e.g., *i*-15:0, a FA with 15 carbon atoms, 0 double bonds and a methyl branch on the second to last carbon atom in the chain). FA data (77 individual FAs) for bearded seals and walruses are provided in Online Resource 1.

We report relative proportions and summed relative proportions of FAs considered to be markers of specific sources (reviewed in Parrish 2013). NMI FAs, which are synthesized exclusively by benthic invertebrate taxa (Paradis and Ackman 1977; Joseph 1982; Kawashima 2005; Barnathan 2009; Monroig et al. 2012), were used as "benthic" markers. The sum of *iso*- and *anteiso*-methyl branched FAs with an odd number of carbon atoms (*ai*-15:0, *i*-15:0, *ai*-17:0, *i*-17:0) was used as a marker of bacteria (Volkman et al. 1980; Budge and Parrish 1998). The bacterial marker, which can be elevated in b-POM relative to i-POM and p-POM, can also vary among benthic invertebrate prey from different feeding guilds (Oxtoby et al. 2016). This makes it a useful trophic marker for examining differences in the types of benthic prey consumed (e.g., subsurface deposit-feeder, mobile predator, and suspension-feeder) and POM sources that sustain those prey. The FAs 16:1n-7, 20:5n-3, and 22:6n-3 are considered to be algal in origin (reviewed in Dalsgaard et al. 2003), so they were used as isotopic end members for compound-specific stable isotope multi-source mixing models.

Additional data sets were provided from other studies (i.e., Wang et al. 2014, 2015a, 2016; Oxtoby et al. 2016) to conduct the analyses described in the following section (*Data analyses*). Benthic invertebrate specimens, and POM samples from ice cores (i-POM), seawater (p-POM), and surface sediment scrapes (b-POM) were collected from the Bering Sea in collaboration with the Bering Sea Ecosystem Study (BEST-BSIERP) in 2009 and 2010. These samples were processed using the same lipid extraction and FA transesterification protocols and instrumentation as described for walrus blubber samples. Additional details regarding sample collection, preparation, and analysis of I-POM and p-POM are detailed in Wang et al. (2014, 2015a). Similar details for b-POM and benthic invertebrate analyses are described in Oxtoby et al. (2016).

Foraging grounds for walruses and bearded seals span the Bering and Chukchi seas (e.g., Lowry et al. 1980; Fay 1982; Jay et al. 2012). Evidence from recent tagging studies indicates overlapping and widespread habitat use throughout the Arctic and sub-Arctic seas by individual walruses (Jay et al. 2012; Quakenbush et al. 2016) and bearded seals (Cameron and Boveng 2009; Cameron et al. 2010); therefore, inclusion of invertebrate specimens and POM samples from the Chukchi and Bering seas was appropriate.

Data analyses

Multivariate non-parametric procedures were performed to describe differences in FA and NMI FA profiles based on 77 FAs that were present in proportions >0.1% of the total between species and by sex within species. FA percentage data were transformed using a $\log(X + 1)$ transformation prior to statistical analysis. We measured differences in profiles using a two-factor nested permutational multivariate analysis of variance (PERMANOVA) with species and sex (nested) as factors. Similarity percentage routines (SIMPER) were employed to identify the FAs that contributed most to dissimilarities in the FA and NMI FA profiles. For this analysis, we removed multivariate outliers

($n = 2$) based on an nMDS biplot and on hunters' observations. Multivariate outliers were male walruses harvested in Savoonga, AK in 2009 and 2010. One walrus was severely emaciated with an empty stomach, while the other walrus appeared healthy. PERMANOVA and SIMPER routines were performed in PRIMER (version 6, Primer-E Ltd). Univariate data met assumptions for parametric analysis, so a two-factor nested ANOVA was used to compare the relative proportions of individual NMI FAs (Fig. 3), the sum of NMI FAs, a composite bacterial marker (sum of *ai*-15:0, *i*-15:0, *ai*-17:0, and *i*-17:0), and δ^{13}C values of algal FAs (16:1n-7, 20:5n-3, and 22:6n-3) between species and by sex (nested) within species. Tukey Honest Significant Differences (HSD) test was performed for pairwise comparisons at a 95% significance level ($\alpha = 0.05$) (R version 3.2.2).

We used a Bayesian mixing model (SIAR, R version 3.2.3) (Parnell et al. 2010) to estimate the proportional contributions of FAs from POM sources (i-POM, p-POM, and b-POM) to walruses and bearded seals. Models were based on δ^{13}C values of the algal FA markers 16:1n-7, 20:5n-3, and 22:6n-3, so we ran four models using varying combinations of δ^{13}C values and models with and without concentration dependencies (Online Resource 2) for comparison (as in Wang et al. 2016). Concentration dependencies account for differences in the relative proportions of individual FA markers in POM sources by weighting the linear mixing model accordingly (Phillips and Koch 2002). We assumed an FA trophic enrichment factor of 0 (Budge et al. 2011; Wang et al. 2016). Male and female walruses were analyzed separately, whereas sexes were combined for bearded seals, because there were no significant differences in FA sources for bearded seals between sexes (see "Results"). Results are presented as means (95% credibility interval) (Bayesian confidence interval).

Walruses and bearded seals consume a wide variety of prey taxa, including benthic invertebrates, demersal, and pelagic prey (e.g., Sheffield and Grebmeier 2009; Huntington and Quakenbush 2013; Crawford et al. 2015). Therefore, we did not use a Bayesian mixing model to estimate the proportional contributions of benthic prey groups as the results would not accurately reflect the full breadth of their diets. Instead, we used δ^{13}C values of algal FAs from benthic invertebrate taxa that are examples of varying feeding types to qualitatively interpret differences in their diets. We compared δ^{13}C values of algal FAs from walruses and bearded seals to those from benthic prey from distinct feeding groups from the Chukchi Sea (an omnivore, a subsurface deposit-feeder, and suspension/surface deposit-feeders) (this study) and the Bering Sea (a predator, a head down deposit-feeder, and suspension/surface and subsurface deposit-feeders) (Oxtoby et al. 2016). Benthic invertebrate specimens from the Chukchi Sea were included in this study to extend the geographic coverage of benthic prey from the Bering Sea (Oxtoby et al. 2016) to known summer feeding grounds for Pacific walruses (e.g., Ray et al. 2006). Given the opportunistic nature of sample collection in the Arctic and sub-Arctic and the limited availability of compound-specific datasets, we were unable to account for interannual differences in δ^{13}C values of benthic prey from the Chukchi and Bering seas. However, mean δ^{13}C values of algal FAs (16:1n-7 and 20:5n-3) from *M. calcarea*, *E. tenuis*, and *N. radiata* collected in 2009–2010 from the Bering Sea (Oxtoby et al. 2016) were similar to those reported in 2012 from the Chukchi Sea (this study) (differences between mean values ranged from 0.4 to 0.7‰ and 0.7 to 1.3‰ for 16:1n-7 and 20:5n-3, respectively).

Results

Fatty acid profiles and markers

FA profiles of walruses and bearded seals were significantly different (PERMANOVA, $P < 0.01$) (Fig. 2). FAs that contributed most to differences between walruses and bearded seals were the NMI FAs 20:2Δ5,11, 22:2Δ7,15, and 24:1, 16:3n-3, 20:2n-9, 23:0, and *ai*-15:0 (SIMPER) (Fig. 2). Additional NMI FAs (22:2Δ7,13, 20:2Δ5,13, and 20:3Δ5,11,14) were among the FAs that collectively contributed up to 45% of the variation in FA profiles between species (Fig. 2). Within species, FA profiles differed between male and female walruses

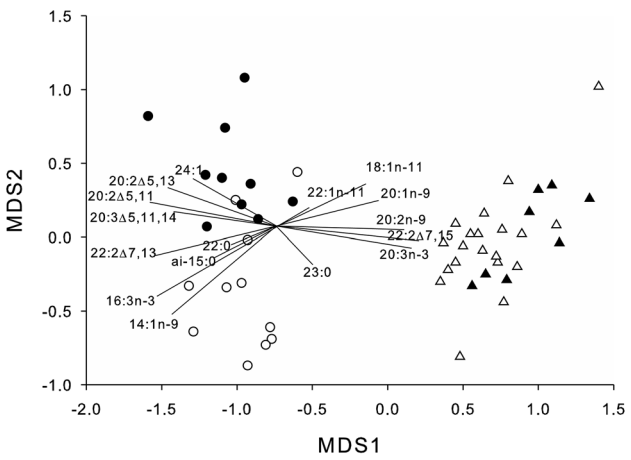

Fig. 2 Non-metric multidimensional scaling plot of male (*filled symbols*) and female (*open symbols*) Pacific walruses (*circles*) and bearded seals (*triangles*). Distances are based on Bray–Curtis similarity matrices using 77 fatty acids occurring in relative proportions >0.1%. Fatty acid vectors displayed are those that contributed most to differences between species and accounted for 45% of the dissimilarity (SIMPER). We set the level of dissimilarity to 45% to include all, but one non-methylene interrupted fatty acid. Vector length and direction correspond to the strength of correlation with nMDS axes. 2D stress = 0.07

(PERMANOVA, $P = 0.03$), but not between male and female bearded seals (PERMANOVA, $P = 0.07$) (Fig. 2).

NMI FA profiles of walruses differed significantly from those of bearded seals (PERMANOVA, $P < 0.01$). Walruses had significantly higher relative proportions of most NMI FAs (20:2Δ5,11, 20:2Δ5,13, 20:3Δ5,11,14, 22:2NMID, and 22:2Δ7,13) than bearded seals (two-factor nested ANOVA, $P < 0.01$) with the exception of 22:2Δ7,15, which was greater in bearded seals (two-factor nested ANOVA, $P < 0.01$) (Table 2; Fig. 3). Due to large relative proportions of 22:2Δ7,15 in bearded seals, the sum of the relative proportions of NMI FAs did not differ between species (two-factor nested ANOVA, $P = 0.10$) (Table 2). Sex-specific differences in NMI FA profiles were detected among walruses (PERMANOVA, $P < 0.01$), but not among bearded seals (PERMANOVA, $P = 0.21$). No significant differences were detected between sexes for either species for five of the six NMI FAs (two-factor nested ANOVA, $P > 0.10$) (Table 2). A significant difference was detected for 22:2NMID between male and female walruses (Tukey HSD test, $P < 0.01$) (Table 2).

The relative proportion of the composite bacterial FA marker was significantly higher in walruses relative to bearded seals (two-factor nested ANOVA, $P < 0.01$) (Table 2); no differences between sexes were detected for either species (two-factor nested ANOVA, $P = 0.90$).

Stable carbon isotope analysis of fatty acids

$\delta^{13}C$ values of algal marker FAs (16:1n-7, 20:5n-3, and 22:6n-3) were higher in bearded seals relative to walruses (two-factor nested ANOVA, $P < 0.01$), but did not vary between sexes in either species (two-factor nested ANOVA, $P > 0.10$) (Fig. 4). Mean $\delta^{13}C$ values of algal FAs ranged from $-28.9 \pm 1.2‰$ (20:5n-3) to $-26.6 \pm 1.1‰$ (22:6n-3) in walruses (mean ± 1SD,

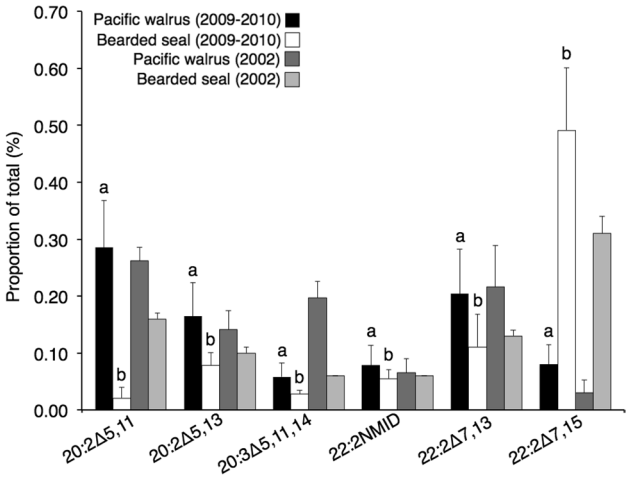

Fig. 3 Relative proportions (% total) of non-methylene interrupted fatty acids in Pacific walruses and bearded seals. Values are means + 1SD, with sexes pooled from 2009 to 2010 (this study) and from 2002 (Budge et al. 2007; Cooper et al. 2009). Letters *a*, *b* indicate significant differences between species (two-factor nested ANOVA, $P < 0.01$). All NMI FA were significantly higher in Pacific walruses than in bearded seals in 2009–2010, with the exception of 22:2D7,15

Table 2 Relative proportions (% total) of benthic fatty acid markers in Pacific walruses and bearded seals, including individual non-methylene interrupted (NMI) fatty acids, their sum, and a composite bacterial fatty acid marker

	Pacific walrus	Bearded seal
20:2Δ5,11	0.29 (0.08)[a]	0.02 (0.02)[b]
20:2Δ5,13	0.16 (0.06)[a]	0.08 (0.02)[b]
20:3Δ5,11,14	0.06 (0.02)[a]	0.03 (0.01)[b]
22:2NMID*	0.08 (0.04)[a]	0.06 (0.02)[b]
22:2Δ7,13	0.20 (0.08)[a]	0.11 (0.06)[b]
22:2Δ7,15	0.08 (0.03)[a]	0.49 (0.11)[b]
Sum (NMI)	0.87 (0.23)[a]	0.78 (0.13)[a]
Sum (Bacterial)	0.97 (0.21)[a]	0.80 (0.09)[b]

Letters a, b indicate significant differences between mean values for each species (two-factor nested ANOVA, $P < 0.01$). Values are means (1SD) with sexes pooled. * 22:2NMID varied significantly between male and female walruses (*NMID* non-methylene interrupted dienoic fatty acid). The composite bacterial marker consists of the sum of the fatty acids *ai*-15:0, *i*-15:0, *ai*-17:0, and *i*-17:0

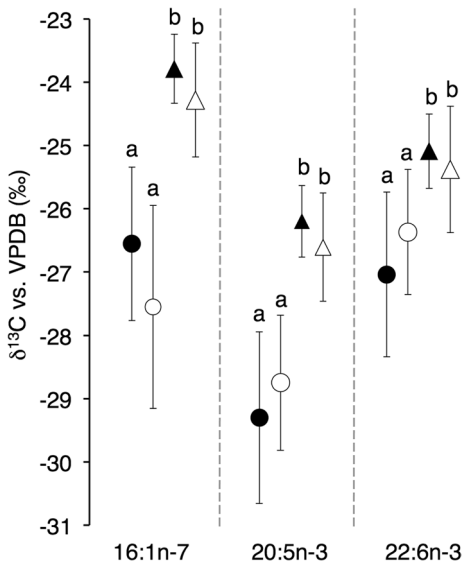

Fig. 4 $\delta^{13}C$ values (‰) for algal marker fatty acids from male (*filled symbols*) and female (*open symbols*) Pacific walruses (*circles*) and bearded seals (*triangles*). Algal marker fatty acids are 16:1n-7, 20:5n-3, and 22:6n-3 (mean ± 1SD). Letters *a*, *b* indicate significant differences between species and sexes (two-factor nested ANOVA, $P < 0.01$). $\delta^{13}C_{FA}$ values were consistently higher in bearded seals than in Pacific walruses

$n = 41$, sexes pooled) and from $-26.5 \pm 0.8‰$ (20:5n-3) to $-24.1 \pm 0.8‰$ (16:1n-7) in bearded seals (mean ± 1SD, $n = 28$, sexes pooled).

We present a range of estimates generated from Bayesian multi-source FA stable isotope mixing models that incorporated various combinations of algal marker FAs and their concentration dependencies (Tables 3; see Online Resource 3 for additional information about sources). The model that used 20:5n-3 and 22:6n-3 provided the most reliable estimates due to greater sample sizes compared with models that included 16:1n-7, which was not always measurable due to GC coelution of monounsaturated and saturated FAs containing 16 carbon atoms. Samples in which coelution occurred were removed from the data set prior to analysis, so model results that included 16:1n-7 had smaller sample sizes (fewer modeled individuals) relative to models without 16:1n-7. Through their diets, walruses and bearded seals obtained substantial contributions of FAs from b-POM [ranging from 44 (17–67)% in walruses to 62 (38–83)% in bearded seals] (Table 3). Bearded seal diets contained lower contributions from p-POM [10 (1–22)%] relative to walruses [51 (32–73%)] (Table 3). Proportional

Table 3 Estimates of the proportional contributions (%) of sympagic, pelagic, and benthic particulate organic matter (i-POM, p-POM, and b-POM, respectively) to consumer diets

i-POM	Pacific walrus (M)	Pacific walrus (F)	Pacific walrus (pooled)	Bearded seal (pooled)
Without				
16:1n-7, 20:5n-3, 22:6n-3	14 (0–28)	19 (0–36)	14 (0–26)	44 (36–52)
16:1n-7, 20:5n-3	26 (4–45)	19 (0–41)	23 (2–40)	44 (33–55)
16:1n-7, 22:6n-3	15 (0–29)	23 (2–42)	15 (2–28)	47 (38–56)
20:5n-3, 22:6n-3	10 (0–23)	17 (4–29)	13 (2–23)	40 (31–49)
With				
16:1n-7, 20:5n-3, 22:6n-3	8 (0–25)	15 (0–37)	14 (0–26)	31 (16–48)
16:1n-7, 20:5n-3	12 (0–36)	13 (0–35)	23 (2–40)	20 (1–64)
16:1n-7, 22:6n-3	15 (0–34)	26 (1–47)	15 (2–28)	18 (8–31)
20:5n-3, 22:6n-3	**7 (0–20)**	**8 (0–19)**	**13 (2–23)**	**27 (15–42)**
p-POM				
Without				
16:1n-7, 20:5n-3, 22:6n-3	37 (6–66)	49 (25–75)	45 (23–70)	5 (0–12)
16:1n-7, 20:5n-3	38 (8–69)	52 (26–80)	53 (27–81)	4 (0–10)
16:1n-7, 22:6n-3	21 (0–42)	37 (10–62)	27 (7–46)	5 (0–13)
20:5n-3, 22:6n-3	67 (41–91)	60 (44–74)	67 (54–80)	15 (3–27)
With				
16:1n-7, 20:5n-3, 22:6n-3	36 (10–60)	46 (20–73)	42 (21–61)	8 (0–17)
16:1n-7, 20:5n-3	42 (14–68)	50 (25–78)	49 (30–68)	5 (0–14)
16:1n-7, 22:6n-3	22 (2–44)	35 (7–62)	23 (4–43)	10 (0–24)
20:5n-3, 22:6n-3	**58 (31–90)**	**47 (27–69)**	**51 (32–73)**	**10 (1–22)**
b-POM				
Without				
16:1n-7, 20:5n-3, 22:6n-3	49 (15–83)	32 (3–57)	41 (13–67)	51 (39–62)
16:1n-7, 20:5n-3	35 (0–69)	28 (0–54)	23 (0–50)	53 (39–66)
16:1n-7, 22:6n-3	64 (35–93)	40 (9–70)	58 (33–83)	48 (35–60)
20:5n-3, 22:6n-3	23 (0–48)	24 (6–41)	20 (5–36)	45 (30–60)
With				
16:1n-7, 20:5n-3, 22:6n-3	56 (28–86)	39 (6–68)	54 (32–76)	61 (37–81)
16:1n-7, 20:5n-3	46 (17–76)	37 (4–63)	47 (26–67)	75 (28–97)
16:1n-7, 22:6n-3	63 (28–94)	39 (4–74)	63 (30–92)	72 (48–90)
20:5n-3, 22:6n-3	**35 (1–62)**	**45 (17–71)**	**44 (17–67)**	**62 (38–83)**

Values are based on stable isotope mixing models run without and with concentration dependencies (Online Resource 3) [means (95% credibility intervals)]. Male (M) and female (F) Pacific walruses were analyzed separately and combined, whereas sexes were combined for bearded seals. We posit that model estimates in bold type are the most reliable estimates based on sample size and incorporation of concentration dependencies

contributions of POM sources were similar between male and female walruses (Table 3). However, Bayesian credibility intervals were larger for walruses relative to bearded seals for POM sources, reflecting greater variation in their $\delta^{13}C$ values of algal marker FAs (Fig. 4).

The stable carbon isotope composition of algal FAs 16:1n-7 and 20:5n-3 from male and female walruses was similar to algal FAs from suspension/surface deposit-feeding bivalves and from an example of a subsurface deposit-feeder (the bivalve *N. radiata*) from the Chukchi and Bering seas (Fig. 5). In contrast, $\delta^{13}C$ values of algal FAs from male and female bearded seals clustered more closely to *Nephtys* spp., a predatory polychaete and *C. opilio*, an epibenthic omnivore (Fig. 5).

Discussion

Walruses and bearded seals collected from 2009 to 2011 had distinct diets consistent with earlier studies (Budge et al. 2007; Cooper et al. 2009). Interspecific dietary differences were revealed by variation in benthic prey taxa, as evidenced by differences in individual benthic FA markers. However, there was no evidence of difference in the sum of all benthic marker FAs between walruses and bearded seals, indicating a similar general reliance on benthic food resources. Benthic POM (b-POM) sources contributed the majority of FAs to the prey taxa that supported walruses and bearded seals; pelagic POM sources contributed an additional substantial source of FAs to the prey resources that supported walruses. We posit that differences in the diets and trophic pathways that sustain walruses and bearded seals resulted from higher predation on surface and subsurface deposit-feeding bivalves by walruses and from higher consumption of predatory and epibenthic omnivorous prey by bearded seals. Relative proportions of benthic marker FAs from this study are consistent with the patterns reported from 2002 (Budge et al. 2007; Cooper et al. 2009), suggesting that resource partitioning between species has not changed over time despite interannual variability documented in bearded seal diets based on their benthic marker FAs (Cooper et al. 2009; Wang et al. 2015b).

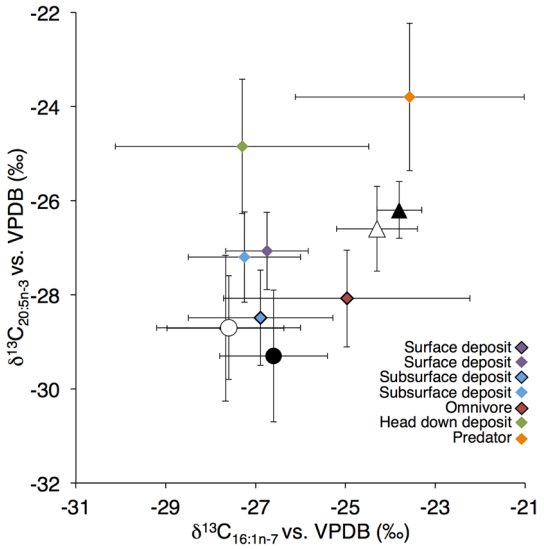

Fig. 5 $\delta^{13}C$ values (‰) of algal marker fatty acids (16:1n-7 and 20:5n-3) from male (*filled symbols*) and female (*open symbols*) Pacific walruses (*circles*) and bearded seals (*triangles*), and benthic invertebrate prey from distinct feeding groups. Prey taxa were collected from the Chukchi Sea (*symbols outlined in black*, this study) and Bering Sea (Oxtoby et al. 2016). Surface deposit = suspension/surface deposit-feeding bivalves *Liocyma fluctuosa*, *Serripes groenlandica*, *Astarte* spp., *Macoma* spp., and *Ennucula tenuis* (this study, covered by female walrus symbol), Surface deposit = *Macoma calcarea* and *Ennucula tenuis* (Oxtoby et al. 2016), subsurface deposit = subsurface deposit-feeding bivalve *Nuculana radiata*, Omnivore = omnivorous crab *Chionoecetes opilio,* Head down deposit = head down deposit-feeding polychaete *Leitoscoloplos pugettensis*, predator = predatory polychaete *Nephtys* spp.

Interspecific and intraspecific variation in diet

Walruses are gregarious animals that travel in large herds and occasionally congregate en masse at terrestrial haul-out sites (Fay 1982; Jay and Fischbach 2008), whereas bearded seals tend to be solitary (Cleator et al. 1989; Simpkins et al. 2003). Increased foraging pressure on localized food resources by walrus herds could oblige individual walruses to consume different prey from one another. In contrast, bearded seals, as solitary individuals, might have a greater ability to forage on a similar variety of preferred food resources, assuming that similar prey distributions are available where individuals forage. We documented higher variation in the stable isotope composition of algal FAs from walruses relative to bearded seals. Differences in dietary breadth do not explain the higher variation, because evidence from stomach content analyses indicates that diets of walruses and bearded seals are characterized by similar breadth (Sheffield and Grebmeier 2009; Quakenbush et al. 2011). Instead, we posit that individual walruses consistently targeted different prey from one another whereas individual bearded seals consistently foraged for similar mixtures of prey relative to one another. These foraging patterns would account for variable $\delta^{13}C$ values of FAs from walruses despite having similar dietary breadth to bearded seals.

Differences in some FA dietary proxies between male and female walruses suggested sex-specific differences in diet, whereas there were no differences in FA dietary proxies between male and female bearded seals. Sexual segregation in summer likely explains dietary differences between male and female walruses (Jay and Hills 2005; Ray et al. 2006). In summer, females and calves migrate northward to the Chukchi Sea, while males migrate south to Bristol Bay

and locations along the Russian coast including the Gulf of Anadyr to forage (Fay 1982; Ray et al. 2006). We suggest that sex-specific differences in FA profiles can be attributed to the incorporation of prey FAs during sexual segregation in the previous summer. Male Walruses feed minimally during the winter reproductive period when females are present, so their blubber may preserve a summer foraging signal (Ray et al. 2006). This would imply a high accumulation of dietary fatty acids during summer months and a slow FA turnover rate, such that dietary differences could be detected during the spring harvest (i.e., up to 6 months after sexual reintegration in late fall). Blubber turnover rates have not been calculated for Pacific walruses or bearded seals. However, blubber turnover rates estimated for adult harp seals (*Phoca groenlandica*) (Kirsch et al. 2000) and newly weaned juvenile harbor seals (*Phoca vitulina richardsi*) (Nordstrom et al. 2008) reveal that turnover is nonlinear and likely occurs on the order of months. A minimum of 3 months was determined for juvenile harbor seals, which is likely an underestimate for adult walruses or bearded seals given the rapid growth characteristic of newly weaned juveniles (Nordstrom et al. 2008).

Differences in diet between sexes could also result from the ability of male walruses to obtain "atypical" prey [e.g., ringed (*Pusa hispida*) and bearded seals] (Lowry and Fay 1984; Huntington and Quakenbush 2013; Seymour et al. 2014b) and from selective foraging by reproductive females for high lipid content prey to support high energetic demands (Noren et al. 2012, 2014). Differential metabolism among males and females may affect FA profiles and $\delta^{13}C$ values of FAs. However, Pacific walruses and bearded seals are unlike certain phocid species that undergo dramatic fluctuations in body condition due to extreme fasting during life history stages like breeding, lactating, and molting. During breeding and molting (March through mid-July for bearded seals and April–August for Pacific walruses), sexes of both species employ a facultative feeding strategy (Fay 1982; Kovacs and Lavigne 1992; Cameron et al. 2010). As a result, we assume the influence of FA catabolism on FA dietary proxies to be minor compared to the influence of diet given intermittent foraging and a dietary signature representative of past foraging recorded in their blubber.

Although walrus and bearded seal diets were characterized by similar proportional contributions of benthic POM, their diets were distinct. FAs from walruses were isotopically similar to those from bivalves from the Chukchi (this study) and Bering seas (Oxtoby et al. 2016), which have been shown to consume organic matter available in surface sediments, irrespective of its origin (Oxtoby et al. 2016). Furthermore, a strong pelagic signal in primary consumers, such as suspension/surface deposit-feeders and subsurface deposit-feeders in the benthic environment, likely results from the dominance of pelagic production to total annual primary production in the Arctic and sub-Arctic marine ecosystem (McRoy and Goering 1976; Gosselin et al. 1997). We attribute dietary differences, including higher proportional contributions of p-POM to walruses relative to bearded seals, to greater consumption of suspension/surface and subsurface deposit-feeding bivalves.

Prey consumed by bearded seals contained lower proportional contributions of pelagic POM relative to those consumed by walruses. Of the prey species described, bearded seals were most isotopically similar to *Nephtys* spp., a mobile predator, and *C. opilio* (snow crab), an omnivore. These species have also been identified as major prey taxa in bearded seal diets based on stomach content analyses (Lowry et al. 1980). Previous research attributed high stable carbon isotope values of FAs ($\delta^{13}C_{FA}$) characteristic of *Nephtys* spp. from the Bering Sea to indirect consumption of i-POM through their prey based on the multi-proxy approach used in this study (Oxtoby et al. 2016). *C. opilio* consumes a broad range of benthic taxa, including bivalves, gastropods, polychaetes, amphipods, and other crustaceans (Kolts et al. 2013a, b; Divine et al. 2015). Carbon isotope ratios of snow crabs (total organic carbon—TOC) were high compared with bivalves (Kolts et al. 2013b), a pattern which is similar to our compound-specific results. However, whether these values reflect an ice algal or benthic signature is unclear. We attribute differences in the proportional contributions of POM sources to bearded seals relative to walruses to higher consumption of predatory and omnivorous invertebrates.

Demersal and pelagic fishes are also important food resources for bearded seals (Lowry et al. 1980; Quakenbush et al. 2011; Crawford et al. 2015). The frequency of occurrence of certain forage fish species, including Arctic Cod (*Boreogadus saida*) and walleye pollock (*Gadus chalcogrammus*), in bearded seal stomachs was greater in recent years (2003–2012) than during a historical period (1975–1984) (Crawford et al. 2015). However, there were no available data sets of $\delta^{13}C_{FA}$ values from adult fishes to elucidate dietary differences that may have resulted from consumption of fishes. Certain forage fish species (e.g., Arctic cod, Canadian eelpout—*Lycodes polaris*, and Longear eelpout—*Lycodes seminudus*) typically have a ratio of 20:1n-9 to 22:1n-11 greater than 1 (Iverson et al. 2002; Falk-Petersen et al. 2004; Dissen 2015), which was characteristic of bearded seals included in this study. Consequently, it is likely that these, and possibly other fish species, may account for part of the dietary signature in bearded seals. Compound-specific stable isotope analysis of additional prey taxa could offer further insight into the relative importance of prey from different feeding groups to the diets of walruses and bearded seals; for example,

shrimp, polychaetes, fish, and bivalve species such as *Mya* spp. that are dominant prey items in bearded seals and walrus stomachs (Lowry et al. 1980; Dehn et al. 2007; Sheffield and Grebmeier 2009).

Proportional contributions of i-POM to bearded seals are lower than recent estimates that also used FA stable isotope mixing models to apportion POM sources to bearded seals (Wang et al. 2016). Our model included a benthic source (b-POM), which is characterized by $\delta^{13}C$ values for 20:5n-3 comparable to those of i-POM, possibly due to isotopic fractionation associated with microbial degradation of algal material (see Sun et al. 2004; Oxtoby et al. 2016 for further discussion of isotopic fractionation of b-POM). Without consideration of differences among FA profiles and individual FA markers which differentiate i-POM and b-POM, a model containing only two sources (i-POM and p-POM) would allocate any contributions from b-POM to i-POM. Indeed, the sum of i-POM and b-POM contributions from our model was roughly equal to the contribution estimated from i-POM alone to bearded seal diets in 2009 and 2010 (Wang et al. 2016).

We interpreted contrasting diets as evidence of resource partitioning, but this conclusion relies on the premise that walrus and bearded seal share the same foraging area. Although specimens were harvested in geographically distinct areas, there is no evidence to suggest that movements of walruses or bearded seals would be confined to harvest locations. Aerial surveys and telemetry data from individuals corroborate ship-based observations and the traditional ecological knowledge describing seasonal migrations and habitat use (Lowry et al. 1980; Fay 1982; Huntington and Quakenbush 2013; Huntington et al. 2016). These studies document widespread habitat use by walruses (Jay et al. 2012; Quakenbush et al. 2016) and bearded seals (Cameron and Boveng 2009; Cameron et al. 2010) in the Bering and Chukchi seas. Factors that may explain patterns in habitat use for walruses include prey availability, bathymetry, and summer ice availability (Jay et al. 2012, 2014). Seasonal movements are similar for bearded seals; however, bearded seals are less reliant on sea ice as a haul-out (Cameron et al. 2010 and references therein).

Conclusions

Walruses and bearded seals had distinct diets in the recent study years. The sum of benthic prey markers did not differ between walruses and bearded seals, supporting the idea that they rely on benthic food resources to a similar extent. However, differences in individual benthic markers indicated that they relied on distinct benthic prey. Walruses and bearded seals were also sustained by two distinct trophic pathways characterized by different contributions of algal organic matter sources to their respective prey; specifically, higher predation on surface and subsurface deposit-feeding bivalves by walruses and higher predation on predatory and epibenthic omnivorous prey by bearded seals. Resource partitioning of benthic invertebrate prey may facilitate the co-occurrence of these two species. Given that the dominant trophic pathways supporting each consumer are distinct, climate-induced changes in algal production in the Arctic could affect walruses and bearded seals differently.

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Author contribution statement LEO wrote the manuscript. SMB, MJW, and LEO formulated the concept. SMB developed methodology for the fatty acid analysis. TS conducted the fieldwork for invertebrate sample collection. LEO and TS performed the fatty acid and compound-specific stable isotope analyses. LEO performed the data analysis based on helpful suggestions from LH, SMB, and DOB. LH, DOB, SWW, TS, and MJW provided substantive editorial advice.

Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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