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Variation in the diet of beluga whales in response to changes in prey availability: insights on changes in the Beaufort Sea ecosystem

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ABSTRACT: The eastern Beaufort Sea (EBS) beluga whale *Delphinapterus leucas* population has experienced a 20 yr decline in inferred growth rates of individuals, which is hypothesized to have resulted from changes in prey availability. We used fatty acid signatures and stable isotope ratios to reconstruct the proportional contributions of 14 prey species to the diets of 178 beluga whales from 2011 to 2014. Prey estimates using quantitative fatty acid signature analysis suggest that EBS beluga whales primarily consume Arctic cod *Boreogadus saida*, a species highly sensitive to climate change. Prey estimates varied with year and sex and size class of the whales, with large males consuming the highest proportions of Arctic cod, and females consuming the highest proportions of capelin *Mallotus villosus*. Estimated proportional contributions of Arctic cod to beluga diet decreased from 2011 to 2014, coinciding with an increase in capelin. Belugas consumed the highest proportions of capelin and the lowest proportions of cod in 2014, the same year in which body condition indices were lowest in the whales. We hypothesize that changing conditions in the Beaufort Sea ecosystem may result in a decreased consumption of Arctic cod by belugas and increased consumption of capelin, which may result in a decline in condition. This may predominately affect females and juveniles since they consume the highest proportions of capelin; however, long-term monitoring is needed for confirmation. Understanding inter-annual variation in prey, and the longer-term nutritional implications of shifting from an Arctic cod- to a capelin-dominated diet should be a priority for monitoring EBS predators.

KEY WORDS: *Delphinapterus leucas* · Arctic change · Marine top predators · Fatty acid signatures · Stable isotope ratios · Marine mammals · Diet estimation · Fishes · Macroinvertebrates

1. INTRODUCTION

Arctic ecosystems are currently undergoing rapid changes, with the Arctic Ocean projected to be free of summer sea ice before 2050 (Stroeve et al. 2007, Wang & Overland 2012, Stroeve & Notz 2018, SIMIP Community 2020). As the most abundant circumpolar Arctic odontocete, the beluga whale *Delphinapterus leucas* is an indicator species for change in Arctic marine ecosystems (Tynan & DeMaster 1997, Laidre 2008, Moore & Huntington 2008, Laidre et al. 2015). The eastern Beaufort Sea (EBS) beluga whale population is one of Canada's largest, with an estimated 40 000 individuals (Allen & Angliss 2015). The EBS population migrates between southwestern Alaskan and Canadian waters (Richard et al. 2001), and arrives

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in the Canadian Beaufort Sea in late May to early June to spend the summer in the Canadian Beaufort Sea and Amundsen Gulf. Calving and nursing occur in early July in and near the Mackenzie Estuary (Richard et al. 2001, Harwood & Smith 2002). Habitat selection of the EBS beluga population is based on sex, size, and reproductive status; large males select offshore pack ice habitat, whereas smaller males and females with young calves select coastal, open-water habitats (Loseto et al. 2006). Recent studies on the EBS beluga whale population have revealed a decline in inferred growth rates of individuals over a 20 yr period, which is hypothesized to have resulted from changing environmental conditions that affected prey availability (Harwood et al. 2014, 2015).

The diets of marine top predators, such as beluga whales, can provide important information on the structure of marine ecosystems. Although most populations of beluga are generalists that feed on a wide variety of prey (Seaman et al. 1982, Quakenbush et al. 2015), the EBS beluga population is hypothesized to specialize on Arctic cod *Boreogadus saida* (Loseto et al. 2009), the most abundant fish species in the Canadian Beaufort Sea (Benoit et al. 2008, Geoffroy et al. 2011, Majewski et al. 2017). *Calanus* markers (C20:1 and C22:1) are the dominant fatty acids in EBS beluga whales, suggesting a diet with a high proportion of Arctic cod (Loseto et al. 2009). However, Arctic cod are highly vulnerable to climate change, particularly in coastal areas of the Beaufort Sea. Negative impacts on growth and physical condition of Arctic cod have been observed at increasing temperature increments (Laurel et al. 2016). As Arctic cod is a main component of energy transfer from plankton to marine mammals and seabirds in many Arctic ecosystems (Welch et al. 1992, 1993, Harter et al. 2013), the northward displacement of Arctic cod could have major impacts on the energy consumption of beluga whales and other marine predators.

As observations of feeding behaviours are difficult to obtain and whales harvested by Inuit subsistence hunters typically have empty stomachs (Harwood & Smith 2002), biomolecular approaches, such as fatty acid signatures and carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios, provide useful information on the prey of whales and other marine mammals (Falk-Petersen et al. 2004, Iverson et al. 2004, Budge et al. 2006, Newsome et al. 2010). Several long-chain (>14 carbons) monounsaturated fatty acids (MUFAs) and polyunsaturated fatty acids (PUFAs) are transferred conservatively from prey to the inner blubber of marine mammals, the most metabolically active layer of the blubber positioned next to the muscle (Iverson et al. 2004, Budge et al. 2006), and are thus representative of the prey consumed. Stable isotope ratios also provide insights into the trophic structure of food webs, since $\delta^{13}C$ values vary with baseline primary production (e.g. benthic vs. pelagic sources) and $\delta^{15}N$ is indicative of trophic position, increasing approximately 3 to 5‰ between trophic levels (Post 2002).

Quantitative fatty acid signature analysis (QFASA), a popular method of diet determination, uses a multivariate model to estimate the relative proportions of prey by minimizing distance measures between the fatty acid signatures of predator and potential prey (Iverson et al. 2004). QFASA has been used to successfully reconstruct the diets of several species of marine mammals, including seals (Budge et al. 2004, Nordstrom et al. 2008, Goetsch et al. 2018) and polar bears *Ursus maritimus* (Thiemann et al. 2008, Bromaghin et al. 2017). To correct for the differential metabolism of fatty acids, QFASA uses calibration coefficients — the ratio of the abundance of each fatty acid in a predator to the average abundance in the diet — which are typically derived from captive studies, where a predator is fed a monotypic diet (Iverson et al. 2004, Nordstrom et al. 2008, Thiemann et al. 2008). Although they have not been derived experimentally for cetaceans, calibration coefficients derived from mink *Mustela vison* best approximated the diets of captive belugas fed primarily herring *Clupea harengus pallasi* (Choy et al. 2019b) and successfully estimated the diets of polar bears (Thiemann et al. 2008, Bromaghin et al. 2017).

The overall objective of our study was to reconstruct prey proportions in the diets of EBS beluga whales and examine inter-annual variation in prey using fatty acid signatures and stable isotope ratios. In collaboration with the Beaufort Regional Environmental Assessment Marine Fishes Project (BREA MFP) survey, we estimated the relative contributions of 14 of the most abundant species (9 fish, 5 invertebrates) in the Canadian Beaufort Sea (e.g. Majewski et al. 2017) to the diets of beluga whales. Our first objectives were to determine if prey species could be differentiated based on: (1) fatty acid signatures and (2) stable isotope ratios. Using lipids as a proxy for energy density, our next objective was to examine differences in lipid content among potential prey species to test the hypothesis that beluga whales prefer energy-dense prey. Finally, we used QFASA to reconstruct the prey contributions to 178 beluga whales sampled from 2011 to 2014 using fatty acid signatures transferred exclusively through diet. We investigated the hypotheses that EBS beluga whales specialized exclusively

on Arctic cod. Using the sex- and size-based habitat groups defined by Loseto et al. (2006, 2008a), we examined whether prey estimates of belugas reflected established differences in habitat use and/or annual variation in environmental conditions.

2. MATERIALS AND METHODS

2.1. Sample collection

Blubber and liver tissue samples were collected from adult beluga whales (n = 178) harvested from July to early August 2011 to 2014 at Inuvialuit beluga hunting camps at Hendrickson Island, Brown's Harbour, Kendall Island, and East Whitefish in the Inuvialuit Settlement Region, Northwest Territories, Canada (Fig. 1). Details of sample collection are described by Choy et al. (2017). Samples were frozen at −20°C in portable freezers on site and then shipped to Fisheries and Oceans Canada in Winnipeg, Manitoba, for laboratory analyses.

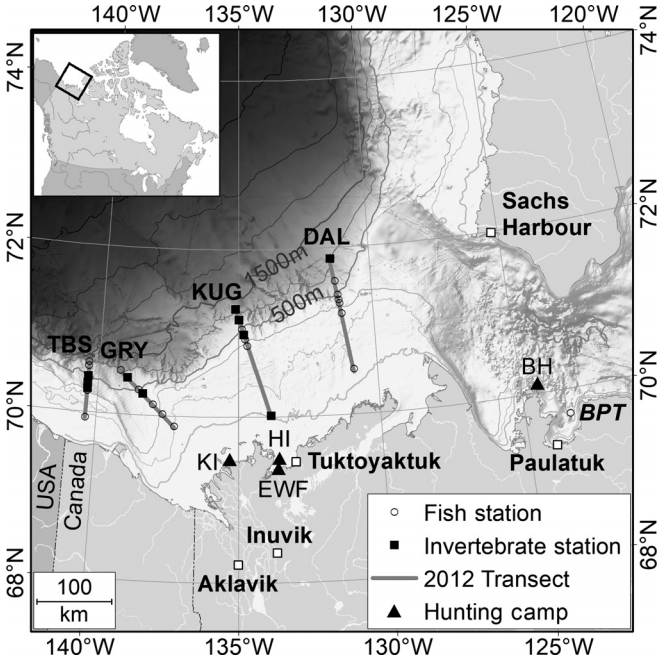

Fig. 1. Study area in the Beaufort Sea ecosystem, including trawling stations for collection of fish species and invertebrate species from the Beaufort Regional Environmental Assessment Marine Fishes Program in 2012. Labelled transects are: transboundary transect (TBS), Garry Island (GRY), Kugmallit Bay (KUG), Dalhousie (DAL), and Bennett Point (*BPT*). Italics represent transect surveyed in 2013. Beluga whale tissues were collected at traditional Inuvialuit hunting camps at Kendall Island (KI), Hendrickson Island (HI), East Whitefish (EWF), and Brown's Harbour (BH) in the Inuvialuit Settlement Region, Northwest Territories, Canada

Fish and macroinvertebrate species were collected from 6 August to 3 September 2012, as part of the BREA MFP. Although we would have preferred to collect species across all years and months to correspond with beluga sampling and the spring–summer diet, this was not feasible due to logistical constraints; thus, we assumed that fatty acid signatures and stable isotope ratios in prey remained consistent across years and seasons. As habitat range varies with body size in beluga whales (Richard et al. 2001, Loseto et al. 2006), prey were selected from different transects, sampling stations, and depths to reflect the spatial variability for beluga foraging. Trawling was conducted at 26 stations at different depths (20–1000 m) across 4 transects in the Canadian Beaufort Sea in 2012 (Fig. 1, Table 1; Majewski et al. 2017). Collected fish included: Arctic cod, Greenland halibut *Reinhardtius hippoglossoides*, Adolf's eelpout *Lycodes adolfi*, Arctic staghorn sculpin *Gymnocanthus tricuspis*, Canadian eelpout *L. polaris*, capelin *Mallotus villosus*, stout eelblenny *Anisarchus medius*, kelp snailfish *Liparis tunicatus*, and Arctic alligatorfish *Aspidophoroides olrikii*. Collected invertebrates included: isopods (*Saduria sabini*), green shrimp *Argis dentata*, circumpolar eualid *Eualus gaimardii gaimardii*, polar shrimp *Sclerocrangon ferox*, and octopus (*Cirroteuthis muelleri*). Most samples were collected on board the

Table 1. Sample size (n), catch depth minimum and maximum, and capture transects of fish and invertebrate species collected as potential prey of eastern Beaufort Sea beluga whales in 2012 and 2013 (capelin only). Transects are: transboundary transect (TBS), Garry Island (GRY), Kugmallit Bay (KUG), Dalhousie (DAL), and Bennett Point (BPT) (see Fig. 1)

Species	n	Depth		Transects
		Min	Max	
Arctic alligatorfish	19	40	75	DAL, GRY, KUG, TBS
Arctic cod	46	18	76	DAL, GRY, KUG, TBS
Arctic staghorn sculpin	19	17	75	DAL, KUG
Adolf's eelpout	31	750	1000	DAL, GRY,
Canadian eelpout	15	17	350	DAL, GRY, KUG
Capelin	16	125	125	BPT
Circumpolar eualid	16	350	350	KUG
Green shrimp	15	200	200	TBS
Greenland halibut	53	350	1000	DAL, GRY, KUG
Isopod	15	40	40	KUG
Kelp snailfish	46	500	850	GRY, TBS
Octopus	16	500	1000	DAL, GRY, KUG, TBS
Polar shrimp	15	350	350	TBS
Stout eelblenny	24	40	40	KUG

FV 'Frosti' using a modified Atlantic Western IIA benthic otter trawl (mesh sizes 90 and 130 mm) or a 3 m benthic beam trawl (mesh sizes 45, 70.5, 100, and 155 mm). Capelin samples were collected using a 3 m beam trawl at Bennett Point (BPT) on 6 August 2013. Fish were sorted and identified on board to species and measured to the nearest 0.1 mm. All fish specimens were adults and had standard lengths greater than 100 mm except for Arctic alligatorfish, which had a maximum standard length of 64 mm. After initial processing (i.e. bulk weight by taxonomic family, length, species identification, etc.), fish were flash frozen at −50°C, then transferred to −30°C for the remainder of the cruise and transit south. They were shipped to DFO Winnipeg frozen and stored at −30°C in well-sealed bags until processing (Budge et al. 2006, Lind et al. 2012, Majewski et al. 2017).

2.2. Fatty acid extraction

Fish and invertebrate samples were whole-body (fish cut in half lengthwise, i.e. dorsum to ventrum) homogenized in a Retsch GM200 grinder in a semi-frozen state, freeze-dried, and then re-frozen and stored at −80°C until fatty acid analysis (Giraldo et al. 2016). Detailed methods for fatty acid extraction for fish and invertebrates are outlined by Giraldo et al. (2016) and for the inner blubber of beluga whales by Choy et al. (2017). In brief, lipids were extracted from 0.5 g of tissue with a 2:1 chloroform:methanol solution containing 0.01% butylated hydroxytoluene using a method modified from Folch et al. (1957) as described by Budge et al. (2006). Percent lipid was determined gravimetrically and recorded as dry weight (g). The extracted lipid was used to prepare the fatty acid methyl esters by transesterification with Hilditch reagent (0.5 N H_2SO_4 in dry methanol). Samples were heated for 1 h at 100°C. Fatty acid methyl ester (FAME) samples were analysed using gas chromatography (Agilent 7890) with a flame ionization detector. Fatty acid standards were obtained from Supelco (37-component FAME mix) and Nuchek (54-component mix GLC-463) and were used to verify the retention times of fatty acid peaks. Fatty acids that were not present in the Supelco standard were quantified using response factors for fatty acids of similar chain length and retention time. In total, 72 fatty acids were identified by retention time based on Supelco and Nu-Chek standards and reported as the percentage of total fatty acids. In our analyses, we used 25 fatty acids identified as being transferred exclusively through diet (Iverson et al. 2004) and with mean percentages above 0.1% (Tables 2 & 3).

2.3. Stable isotope analysis

Liver tissue samples (approximately 0.5 g) for beluga whales, whole body tissues for invertebrates, and dorsal muscle tissues for fish were freeze-dried for at least 48 h and analysed for C and N stable isotope ratios at the University of Waterloo Environmental Isotope Laboratory. Full methods are described by Stasko et al. (2016) and Choy et al. (2016). Machine analytical precision was ±0.1‰ and ±0.2‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, and was determined by repeat analysis of duplicates (1 in 10). All measurements were expressed using standard delta (δ) notation as per mil differences (‰) with respect to the international reference standards Vienna Peedee Belemnite for $\delta^{13}C$ (Craig 1957) and nitrogen gas in the atmosphere for $\delta^{15}N$ (Mariotti 1983).

Quality control was monitored and corrections were made using international reference materials and in-house standards that were calibrated using certified international reference materials (i.e. IAEA-N1 + N2, IAEA-CH3 + CH6, USGS-41 + 41), with an analytical error of 0.2‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$ required for reportable data. National Institute of Standards and Technology standard 1577B (bovine liver) was used as a post-correction check throughout the analysis. Approximately 20% of the total sample number was comprised of standards or reference materials.

Since differences among taxa in lipid and inorganic carbonate content can affect the interpretation of $\delta^{13}C$ values, capelin and invertebrate tissues were treated for lipids and carbonates (for species with exoskeletons), respectively, following methods described by Choy et al. (2016). For beluga liver tissues, a lipid correction model ($\delta^{13}C_{extracted} = -1.868 + 0.839 \times \delta^{13}C_{bulk}$) derived by Choy et al. (2016) was used to correct bulk $\delta^{13}C$ values. Bulk $\delta^{13}C$ values in fish were corrected using the lipid normalization model of Choy et al. (2016) for capelin based on C:N ratios: $\Delta^{13}C = -2.82 + 0.99 \times C{:}N$, which is similar to the lipid normalization model of Post et al. (2007) for aquatic animals ($\Delta^{13}C = -3.32 + 0.99 \times C{:}N$). Bulk untreated samples were used for $\delta^{15}N$ values for all species.

2.4. Data analysis of lipids and dietary tracers

Correspondence analysis was performed on untransformed data to compare fatty acid signatures

Table 2. Mean percent fatty acid (FA) signatures of potential fish prey of beluga whales. Only FAs that contribute to more than 1% of the total percent FAs are shown. SFA: saturated fatty acid, MUFA: monounsaturated fatty acid, PUFA: polyunsaturated fatty acids. **Bold** indicates the 25 FAs used to generate diet estimates. Values are given as mean ± 1 SE

FAs	Adolf's eelpout	Arctic alligatorfish	Arctic cod	Canadian eelpout	Capelin	Greenland halibut	Stout eelbenny	Arctic stag-horn sculpin	Kelp snailfish
SFAs									
14:0	1.95 ± 0.1	1.94 ± 0.1	3.77 ± 0.1	3.69 ± 0.2	6.28 ± 0.1	3.51 ± 0.1	3.86 ± 0.1	3.13 ± 0.19	2.77 ± 0.1
16:0	12.86 ± 0.3	14.51 ± 0.2	11.86 ± 0.3	13.28 ± 0.4	10.79 ± 0.3	12.01 ± 0.3	15.29 ± 0.2	14.72 ± 0.3	10.51 ± 0.2
18:0	2.75 ± 0.2	4.16 ± 0.2	1.46 ± 0.1	2.42 ± 0.1	0.73 ± 0.0	2.33 ± 0.0	2.99 ± 0.1	2.93 ± 0.1	1.94 ± 0.1
MUFAs									
16:1n-7	16.27 ± 1.6	17.76 ± 1.1	17.39 ± 0.4	27.27 ± 2.1	18.02 ± 0.6	14.40 ± 0.2	17.98 ± 0.9	21.49 ± 1.8	9.52 ± 0.3
18:1n-9	13.22 ± 0.4	11.28 ± 0.5	5.95 ± 0.2	7.99 ± 0.3	5.89 ± 0.2	16.50 ± 0.3	11.74 ± 0.2	10.98 ± 0.5	13.23 ± 0.4
18:1n-7	7.51 ± 0.2	11.38 ± 0.3	4.04 ± 0.2	8.59 ± 0.3	2.68 ± 0.1	4.82 ± 0.1	7.08 ± 0.2	9.95 ± 0.2	6.46 ± 0.1
20:1n-11	0.83 ± 0.1	1.16 ± 0.1	0.87 ± 0.0	0.19 ± 0.0	0.79 ± 0.1	0.93 ± 0.0	0.40 ± 0.0	0.46 ± 0.1	2.02 ± 0.1
20:1n-9	3.84 ± 0.2	0.97 ± 0.1	10.27 ± 0.6	1.05 ± 0.1	13.02 ± 0.4	12.14 ± 0.3	1.25 ± 0.1	1.59 ± 0.2	10.05 ± 0.3
20:1n-7	1.52 ± 0.1	4.93 ± 0.5	3.12 ± 0.5	1.12 ± 0.1	2.00 ± 0.2	1.39 ± 0.2	1.12 ± 0.0	1.23 ± 0.1	1.58 ± 0.1
22:1n-11	1.37 ± 0.1	0.10 ± 0.0	11.40 ± 0.6	0.30 ± 0.1	13.23 ± 0.6	6.95 ± 0.2	0.63 ± 0.1	0.43 ± 0.1	2.78 ± 0.2
22:1n-9	0.77 ± 0.0	0.31 ± 0.0	3.82 ± 0.4	0.23 ± 0.0	2.08 ± 0.1	1.92 ± 0.0	0.42 ± 0.0	0.48 ± 0.1	1.35 ± 0.1
22:1n-7	0.19 ± 0.0	0.97 ± 0.2	1.03 ± 0.1	0.12 ± 0.0	0.73 ± 0.0	0.32 ± 0.0	0.15 ± 0.0	0.11 ± 0.0	0.20 ± 0.0
PUFAs									
16:2n-6	0.20 ± 0.0	0.40 ± 0.0	0.09 ± 0.0	0.17 ± 0.0	0.15 ± 0.0	0.12 ± 0.0	0.29 ± 0.0	0.21 ± 0.0	0.14 ± 0.0
16:2n-4	0.18 ± 0.0	0.24 ± 0.0	0.56 ± 0.0	0.74 ± 0.1	0.47 ± 0.0	0.31 ± 0.0	0.28 ± 0.0	0.40 ± 0.0	0.21 ± 0.0
16:3n-4	0.04 ± 0.0	0.06 ± 0.0	0.23 ± 0.0	0.47 ± 0.1	0.32 ± 0.0	0.08 ± 0.0	0.10 ± 0.0	0.11 ± 0.0	0.04 ± 0.0
18:2n-6	0.93 ± 0.0	0.59 ± 0.0	0.53 ± 0.0	0.61 ± 0.0	1.12 ± 0.1	0.67 ± 0.0	0.95 ± 0.0	0.70 ± 0.0	0.88 ± 0.0
18:2n-4	0.09 ± 0.0	0.09 ± 0.0	0.14 ± 0.0	0.16 ± 0.0	0.09 ± 0.0	0.09 ± 0.0	0.08 ± 0.0	0.15 ± 0.0	0.10 ± 0.0
18:3n-6	0.15 ± 0.0	0.07 ± 0.0	0.10 ± 0.0	0.24 ± 0.0	0.12 ± 0.0	0.10 ± 0.0	0.12 ± 0.0	0.13 ± 0.0	0.06 ± 0.0
18:3n-4	0.06 ± 0.0	0.08 ± 0.0	0.04 ± 0.0	0.09 ± 0.0	0.05 ± 0.0	0.05 ± 0.0	0.03 ± 0.0	0.11 ± 0.0	0.06 ± 0.0
18:3n-3	0.25 ± 0.0	0.16 ± 0.0	0.25 ± 0.0	0.16 ± 0.0	0.50 ± 0.0	0.22 ± 0.0	0.61 ± 0.0	0.20 ± 0.0	0.36 ± 0.0
18:4n-3	0.30 ± 0.0	0.19 ± 0.0	0.60 ± 0.0	0.93 ± 0.1	0.89 ± 0.1	0.45 ± 0.0	1.11 ± 0.1	0.39 ± 0.0	0.54 ± 0.0
18:4n-1	0.02 ± 0.0	0.04 ± 0.0	0.12 ± 0.0	0.11 ± 0.0	0.09 ± 0.0	0.06 ± 0.0	0.07 ± 0.1	0.10 ± 0.0	0.04 ± 0.0
20:2n-6	0.37 ± 0.0	0.20 ± 0.0	0.16 ± 0.0	0.17 ± 0.0	0.18 ± 0.0	0.24 ± 0.0	0.28 ± 0.0	0.22 ± 0.0	0.24 ± 0.0
20:3n-6	0.10 ± 0.0	0.13 ± 0.0	0.04 ± 0.0	0.09 ± 0.0	0.03 ± 0.0	0.06 ± 0.0	0.05 ± 0.0	0.09 ± 0.0	0.05 ± 0.0
20:3n-3	0.18 ± 0.0	0.09 ± 0.0	0.04 ± 0.0	0.05 ± 0.0	0.10 ± 0.0	0.12 ± 0.0	0.08 ± 0.0	0.10 ± 0.0	0.08 ± 0.0
20:4n-6	3.94 ± 0.3	2.22 ± 0.2	0.30 ± 0.0	2.22 ± 0.2	0.21 ± 0.01	0.58 ± 0.0	1.49 ± 0.1	2.30 ± 0.2	0.85 ± 0.1
20:4n-3	0.15 ± 0.0	0.23 ± 0.0	0.26 ± 0.0	0.26 ± 0.0	0.29 ± 0.0	0.25 ± 0.0	0.16 ± 0.0	0.29 ± 0.0	0.30 ± 0.0
20:5n-3	9.86 ± 0.2	9.23 ± 0.4	8.19 ± 0.3	14.10 ± 1.2	5.42 ± 0.3	5.18 ± 0.1	12.29 ± 0.2	10.27 ± 0.8	10.55 ± 0.4
21:5n-3	0.09 ± 0.0	0.13 ± 0.0	0.14 ± 0.0	0.25 ± 0.0	0.14 ± 0.0	0.13 ± 0.0	0.12 ± 0.0	0.16 ± 0.0	0.14 ± 0.0
22:5n-6	0.41 ± 0.0	0.23 ± 0.0	0.06 ± 0.0	0.57 ± 0.1	0.07 ± 0.0	0.08 ± 0.0	0.30 ± 0.0	0.49 ± 0.0	0.13 ± 0.0
22:5n-3	1.12 ± 0.1	1.63 ± 0.1	0.80 ± 0.0	0.79 ± 0.1	0.65 ± 0.0	1.10 ± 0.0	1.01 ± 0.0	1.80 ± 0.1	0.78 ± 0.0
22:6n-3	9.77 ± 0.7	5.96 ± 0.6	6.03 ± 0.4	5.24 ± 0.4	6.56 ± 0.6	6.82 ± 0.2	10.48 ± 0.3	7.46 ± 0.6	12.18 ± 0.5
∑25 FAs	35.62 ± 2.0	28.75 ± 2.2	48.39 ± 3.2	29.63 ± 2.6	48.64 ± 2.5	39.24 ± 1.2	32.87 ± 1.0	28.16 ± 2.4	44.88 ± 1.9
∑32 FAs	91.31 ± 5.0	91.41 ± 4.9	93.65 ± 4.6	93.66 ± 6.2	93.67 ± 3.8	93.91 ± 2.2	92.81 ± 2.7	93.15 ± 5.7	90.08 ± 3.1

among all species using the package 'ade4' (Chessel et al. 2004) and visualized using 'ggord' (Beck 2017) in R 3.4.4 (R Core Team 2018). Correspondence is an exploratory technique that calculates a chi-squared (inertia) distance matrix to define the relationship between individuals and fatty acids, and is visualized in 2-dimensional space (Greenacre & Primicerio 2013). Biplots, created using SigmaPlot Version 12.0 (Systat Software),were used to visualize the relationship between stable isotope values of belugas and their potential prey. To determine if we could distinguish among prey sources using fatty acid signatures and stable isotope ratios, we used a 1-way permutational multivariate ANOVA (PERMANOVA) test followed by post hoc pairwise tests separately for each species. Each procedure tests different properties of the data; the null hypothesis of PERMANOVA is that centroids of the groups as defined in the chosen distance measure are equivalent (Anderson & Walsh 2013). Factors were fixed (not random) in the PERMANOVA, and Type III sums of squares were used. Significance was determined using 9999 unrestricted permutations of the raw data and Monte Carlo p-values when the number of unique permutations was <200. The *a priori* significance level was $\alpha = 0.05$ for all statistical procedures. PERMANOVA is not affected by violations in normality, but may be sensitive to dispersions of multivariate data

Table 3. Mean percent fatty acid signatures of beluga whales and their potential invertebrate prey. Other details as in Table 2

FAs	Beluga whale	Circumpolar eualid	Green shrimp	Isopod	Octopus	Polar shrimp
SFAs						
14:0	5.57 ± 0.1	2.01 ± 0.1	1.39 ± 0.1	1.62 ± 0.2	2.09 ± 0.3	1.22 ± 0.1
16:0	7.83 ± 0.1	13.15 ± 0.5	13.71 ± 0.6	12.86 ± 0.4	13.52 ± 0.6	14.39 ± 0.5
18:0	1.80 ± 0.0	2.14 ± 0.1	1.61 ± 0.1	2.24 ± 0.3	3.63 ± 0.2	1.88 ± 0.1
MUFAs						
16:1n-7	12.97 ± 0.3	17.18 ± 1.3	14.25 ± 1.3	33.39 ± 3.4	9.33 ± 1.6	14.04 ±1.1
18:1n-9	10.68 ± 0.2	7.89 ± 0.3	6.41 ± 0.5	8.15 ± 0.9	8.45 ± 1.5	6.85 ± 0.5
18:1n-7	3.63 ± 0.0	10.34 ± 0.2	11.70 ± 0.2	8.09 ± 0.7	9.78 ± 1.2	12.51 ±0.3
20:1n-11	5.17 ± 0.1	0.64 ± 0.1	0.95 ± 0.1	0.76 ± 0.1	0.97 ± 0.1	0.65 ± 0.1
20:1n-9	11.82 ± 0.2	1.87 ± 0.2	0.61 ± 0.0	0.65 ± 0.1	9.66 ± 0.6	0.66 ± 0.1
20:1n-7	1.24 ± 0.0	1.31 ± 0.1	1.35 ± 0.2	2.03 ± 0.3	1.50 ± 0.2	1.02 ± 0.2
22:1n-11	11.30 ± 0.2	1.46 ± 0.2	0.16 ± 0.0	0.41 ± 0.1	2.08 ± 0.4	0.26 ± 0.1
22:1n-9	2.61 ± 0.1	0.46 ± 0.1	0.14 ± 0.0	0.16 ± 0.0	2.00 ± 0.2	0.16 ± 0.0
22:1n-7	0.61 ± 0.0	0.48 ± 0.0	0.42 ± 0.0	0.31 ± 0.0	0.39 ± 0.1	0.55 ± 0.1
PUFAs						
16:2n-6	0.10 ± 0.0	0.43 ± 0.0	0.61 ± 0.0	0.22 ± 0.0	0.20 ± 0.0	0.44 ± 0.0
16:2n-4	0.52 ± 0.0	0.25 ± 0.0	0.11 ± 0.0	0.29 ± 0.0	0.03 ± 0.0	0.08 ± 0.0
16:3n-4	0.15 ± 0.0	0.05 ±0.0	0.03 ± 0.0	0.11 ± 0.0	0.12 ± 0.0	0.01 ± 0.0
18:2n-6	0.71 ± 0.0	0.73 ± 0.0	0.64 ± 0.0	0.73 ± 0.0	0.22 ± 0.0	0.52 ± 0.0
18:2n-4	0.09 ± 0.0	0.13 ± 0.0	0.12 ± 0.0	0.12 ± 0.0	0.08 ± 0.0	0.11 ± 0.0
18:3n-6	0.08 ± 0.0	0.18 ± 0.0	0.11 ± 0.0	0.20 ± 0.0	0.06 ± 0.0	0.08 ± 0.0
18:3n-4	0.11 ± 0.0	0.09 ± 0.0	0.13 ± 0.0	0.14 ± 0.0	0.08 ± 0.0	0.11 ± 0.0
18:3n-3	0.24 ± 0.0	0.33 ± 0.0	0.23 ± 0.0	0.31 ± 0.1	0.22 ± 0.0	0.18 ± 0.0
18:4n-3	0.39 ± 0.0	0.53 ± 0.1	0.12 ± 0.0	0.41 ± 0.1	0.11 ± 0.0	0.11 ± 0.0
18:4n-1	0.08 ± 0.0	0.03 ± 0.0	0.03 ± 0.0	0.03 ± 0.0	0.05 ± 0.0	0.02 ± 0.0
20:2n-6	0.20 ± 0.0	0.30 ± 0.0	0.31 ± 0.0	0.33 ± 0.0	1.05 ± 0.1	0.21 ± 0.0
20:3n-3	0.04 ± 0.0	0.14 ± 0.0	0.07 ± 0.0	0.08 ± 0.0	0.93 ± 0.3	0.05 ± 0.0
20:3n-6	0.09 ± 0.0	0.10 ± 0.0	0.15 ± 0.0	0.19 ± 0.0	0.09 ± 0.0	0.13 ± 0.0
20:4n-6	0.26 ± 0.0	1.96 ± 0.1	2.53 ± 0.1	3.54 ± 0.5	2.92 ± 0.6	2.45 ± 0.2
20:4n-3	0.31 ± 0.0	0.21 ± 0.0	0.24 ± 0.0	0.15 ± 0.0	0.15 ± 0.0	0.18 ± 0.0
20:5n-3	2.69 ± 0.1	16.68 ± 1.0	19.90 ± 0.9	10.24 ± 1.4	10.43 ± 2.0	18.81 ± 0.7
21:5n-3	0.17 ± 0.0	0.17 ± 0.0	0.22 ± 0.0	0.12 ± 0.0	0.09 ± 0.0	0.19 ± 0.0
22:5n-6	0.12 ± 0.0	0.22 ± 0.0	0.39 ± 0.0	0.44 ± 0.2	0.21 ± 0.0	0.32 ± 0.0
22:5n-3	3.46 ± 0.1	1.73 ± 0.1	3.03 ± 0.1	0.77 ± 0.1	0.55 ± 0.1	3.01 ± 0.1
22:6n-3	6.92 ± 0.1	10.19 ± 0.8	10.14 ± 1.0	4.18 ± 0.8	11.46 ± 2.7	12.25 ± 0.9
∑25 FAs	46.01 ± 1.0	38.92 ± 3.0	39.72 ± 2.7	26.13 ± 3.7	45.08 ± 7.7	39.56 ± 2.6
∑32 FAs	91.95 ± 1.7	93.36 ± 5.6	91.83 ± 5.6	93.25 ±9.7	92.44 ± 13.2	93.46 ± 5.2

(although differences in dispersion are not substantial enough to inflate the error rates of PERMANOVA; Anderson et al. 2008). A 1-way similarity percentage (SIMPER) routine was used to identify which fatty acids contributed most to dissimilarities among prey. SIMPER first tabulates fatty acid contributions to the average similarity within a species followed by the average dissimilarity between species (Clarke et al. 2014, Clarke & Gorley 2015). We designated a cut-off of fatty acids that characterized up to 80% of dissimilarities. Multivariate significance tests were performed using PRIMER v.7.0 and PERMANOVA+. A 1-way ANOVA followed by a Tukey honestly significant difference (HSD) test were used to examine differences in % lipid among fish and invertebrates. Percentage data were square-root transformed for analysis to meet assumptions of normality of residuals and homogeneity of variances.

2.5. Calibration coefficients

Fatty acid signatures vary in their fractionation or turnover rates across different tissues and species; thus, an understanding of the fractionation rates is important for identifying the approximate timeframe of prey consumption represented by these tracers. Fatty acid signatures in the inner blubber of newly weaned harbor seals *Phoca vitulina* are representative of prey consumed 1.5 to 3 mo prior (Nordstrom et al. 2008), and a recent study on diet reconstruction in captive beluga whales estimated that fatty acid signatures in the inner blubber represented prey consumed approximately 2 wk to 1 mo before sampling (Choy et al. 2019b). As our sampling was conducted in July, we assumed that the fatty acid signatures in the inner blubber of beluga whales had a turnover rate of approximately 2 to 5 wk and were representative of the spring–summer diet of the whales in the Canadian Beaufort Sea. To correct for the differential metabolism of fatty acids, our QFASA model used calibration coefficients derived from mink that were fed herring supplemented with seal oil (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m647p195_supp.pdf; Thiemann et al. 2008); these are the calibration coefficients that best estimated the diets of captive beluga whales (Choy et al. 2019b).

2.6. QFASA diagnostics and diet estimation

Using a script provided by Bromaghin (2017a) with default settings, proportional contributions of prey to 178 individual beluga whales were estimated. The

QFASA in R package v.1.2.0 (QFASAR; Bromaghin 2017b) implemented in R 3.4.4 (R Core Team 2018) was applied with 12 prey groups (decapods as 1 class). To evaluate the performance of the prey library, we conducted a leave-one-prey-out analysis. Briefly, each prey type was temporarily removed from the library and its signature was re-modelled and diet estimated as if it were the predator. An average proportion of 1.0 indicates a prey that was highly identifiable, whereas values less than 1.0 indicate misallocation (Bromaghin et al. 2016a).

Using the 'diet_est$est_ind' function, the diets of individual beluga whales were estimated in the predator space using Aitchison distance measures; distances between the observed and modelled predator signatures were minimized (Iverson et al. 2004, Bromaghin et al. 2013, 2015). Bootstrap sampling (n = 100) was used to estimate the variance matrix of individual diet composition for each whale, for which the signatures of each prey were independently sampled with replacement to construct a prey library. The variance and covariance of the replicated prey estimates were used to create a variance matrix for the proportional contributions of each prey to the diets of individual whales (Beck et al. 2007, Bromaghin et al. 2015). To provide insights into the reliability of diet estimates, we examined the predator proportions that fell outside the range of mean prey proportions using the function 'pred_beyond_prey()', which may indicate a violation of one or both of the primary model assumptions (Bromaghin et al. 2015, 2016a).

To test if the diets of belugas reflect inter-annual differences in habitat use selection, we ran a 2-factor PERMANOVA following procedures outlined by Choy et al. (2017). The first factor was year, and habitat selection was defined by sex–size classes; females (n = 26) were kept as 1 group and males (n = 152) were divided into 3 size classes sized defined by Loseto et al. (2008a): small males (<3.8 m total body length) that use coastal habitat, medium-sized males (3.8–4.2 m) that use mixed sea ice, and large males (>4.2 m) that select pack ice. Boxplots for diet estimates and lipid content were created using SigmaPlot Version 12.0 (Systat Software).

3. RESULTS

3.1. Dietary tracers and lipid content of beluga prey

Correspondence analysis of the 25 dietary fatty acids from the inner blubber layer of beluga whales, and from fish and invertebrate prey, explained 71.5% (Fig. 2A,B) and 81.3% (Fig. 2C,D) of the variance, respectively. Fish and invertebrate species on the right axis had a higher proportion of benthic markers (e.g. 20:4n6), while species on the left axis had a higher proportion of pelagic markers (e.g. 20:1 and 22:1 MUFAs; Fig. 2B,D). The fatty acids of fish and invertebrates differed significantly among species (PERMANOVA; 25 fatty acids, pseudo-F_{13} = 51.7, p < 0.01). All pairwise species comparisons were significantly different (p < 0.04) except for the comparisons between green and polar shrimp (t = 1.37, p = 0.17), and between octopus and kelp snailfish (t = 1.25, p = 0.20). Six fatty acids contributed up to 80% of the dissimilarities among species: 20:1n-7, 20:1n-9, 20:4n-6, 20:5n-3, 22:1n-11, 22:6n-3 (SIMPER; Table S2).

The mean δ^{15}N (18.12‰) and δ^{13}C (–19.52‰) values of beluga whales were higher than all fish and invertebrate species (mean range δ^{15}N: 12.24 to 17.71‰; δ^{13}C: –23.03 to –20.72‰; Fig. 3). Stable isotope ratios of potential prey also differed significantly among species (PERMANOVA, pseudo-F_{13} = 55.94, p < 0.01). Most pairwise comparisons were significantly different (PERMANOVA p < 0.01), except for the comparisons between Arctic alligatorfish and Arctic staghorn sculpin (PERMANOVA pairwise test; t = 1.62, p = 0.09), Arctic alligatorfish and Greenland halibut (t = 1.60, p = 0.09), Canadian eelpout and octopus (t = 1.48, p = 0.12), green shrimp and polar shrimp (t = 1.08, p = 0.31), and circumpolar eualid and capelin (t = 1.39, p = 0.15).

Prey species differed significantly in lipid content (1-way ANOVA, $F_{13,276}$ = 34.76, p < 0.01), with Arctic cod (mean ± SD: 33.4 ± 10.7% dry weight), Greenland halibut (33.2 ± 7.8%), and capelin (31.3 ± 6.1%) having significantly higher lipid content than all other prey except Canadian eelpout (Tukey HSD test; Table S3, Fig. 4). Benthic invertebrates and specifically isopods (6.7 ± 3.9%) had the lowest lipid content of all species.

3.2. QFASA diagnostics and diet estimation

Based on our PERMANOVA and correspondence analysis, we combined the 3 decapod species into 1 group in our QFASA prey library. According to our leave-one-prey-out analysis, the fatty acid signatures of prey separated with low misallocations, with some misidentification of Arctic staghorn sculpin as Canadian eelpout and Adolf's eelpout, and isopods as decapods and Arctic staghorn sculpin (Table S4). Because there was low misclassification of Canadian eelpout and decapods with other groups, and due to

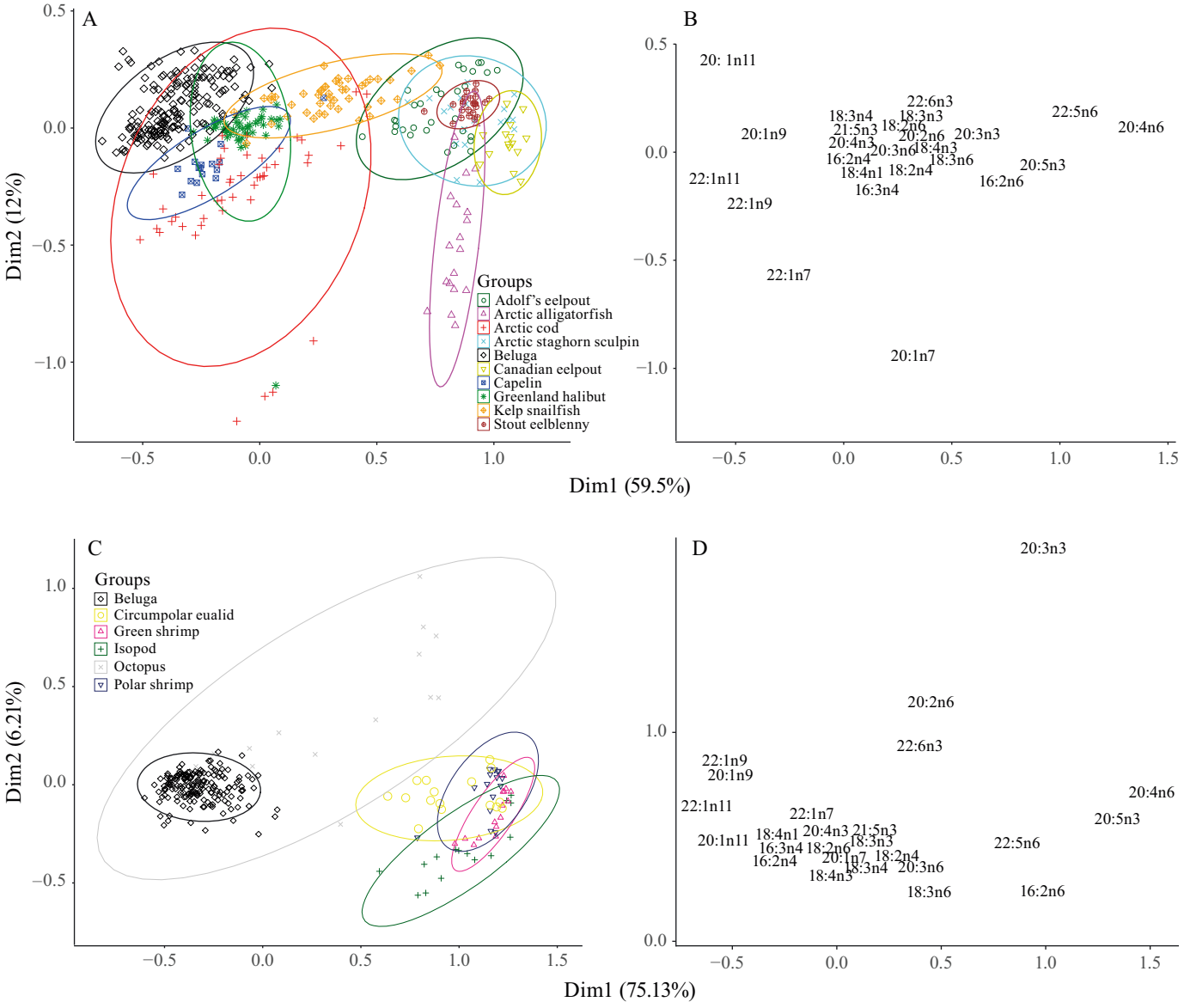

Fig. 2. Correspondence analysis of fatty acid signatures from the inner blubber of Beaufort Sea beluga whales (n = 178) and potential prey species. (A) Individual fish and (B) their 25 main dietary fatty acid signatures. (C) Individual invertebrates and (D) their 25 main dietary fatty acid signatures. The ellipses show the 95% confidence regions for the mean for each species

biological differences among these species, we kept our analysis to 12 prey groups.

Results from QFASAR using 25 fatty acids indicated that across all individual whales (n = 178; Table S5), Arctic cod was the most dominant prey item (59.5 ± 7.1% [SE]) followed by capelin (18.6 ± 5.5%) and Canadian eelpout (14.0 ± 2.1%). Greenland halibut (4.0 ± 1.7%), kelp snailfish (2.2 ± 1.0%), and decapods (1.1 ± 0.4%) were estimated to be minor components of beluga diet. Of all predator fatty acids, 35.6% were outside of the range of mean prey proportions with apparent mismatches for 22:1n-11, which also contributed the second largest proportion to the minimized distance (Fig. S1, Table S6), but only 7.6% of fatty acids of predators were outside of the individual prey proportions.

Diet proportions of beluga whales differed among years (2-way PERMANOVA, pseudo-$F_{3,162}$ = 6.3, p < 0.01) and among sex and size classes (pseudo-$F_{3,162}$ = 5.9, p < 0.01), but there was no significant interaction (pseudo-$F_{9,162}$ = 1.2, p = 0.30). According to SIMPER, proportions of Arctic cod and capelin accounted for approximately 80% of the differences in beluga prey across sex and size classes and years (Table S7). The diets of large males differed from medium (t = 2.1, p = 0.03) and small males (t = 3.7, p < 0.01), as well as

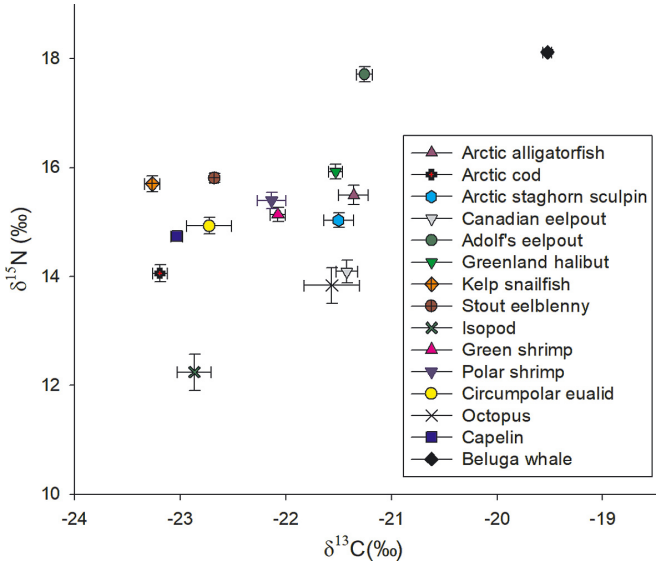

Fig. 3. Mean carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios of Beaufort Sea beluga whale liver tissues and potential prey species with ±1 SE bars

from females ($t = 3.0$, $p < 0.01$); large males consumed the highest percentage of Arctic cod (71.1 ± 6.5%) and Greenland halibut (7.3 ± 1.7%) and the lowest proportion of capelin (9.0 ± 4.0%) relative to the other sex and size classes (Fig. 5). The diets of medium-sized males differed from small males (t = 2.2, p = 0.02). There were no differences in diets between females and either medium-sized males (t = 1.7, p = 0.07) or small males (t = 0.3, p = 0.94), although females consumed the highest proportion of capelin (females: 34.4 ± 8.3%) and the lowest proportion of Arctic cod (36.5 ± 10.2%) relative to all males.

Among years, inferred diets differed between 2014 and all other years (2011: $t = 4.1$, $p < 0.01$; 2012: t = 2.7, $p < 0.01$; 2013: $t = 2.3$, $p = 0.01$). Whales from 2014 consumed the lowest percentage of Arctic cod (Fig. 6; 47.8 ± 8.4%) and the highest proportions of capelin (29.2 ± 7.0%) relative to whales in 2012 (cod: 62.3 ± 8.4%; capelin: 18.5 ± 6.0%), 2013 (60.2 ± 5.9%; 17.0 ± 3.6%), and 2011 (73.9 ± 6.5%; 3.2 ± 3.0%). Diet estimates also differed between 2011 and 2013 ($t = 2.8$, $p < 0.01$), with whales from 2011 consuming a higher percentage of Canadian eelpout (17.5 vs. 13.3%), but lower percentages of Greenland halibut (2.7 vs. 6.2%), decapods (0.2 vs. 1.4%), and capelin. There were no differences in prey proportions between 2011 and 2012 ($t = 1.6$, $p = 0.10$) or between 2012 and 2013 ($t = 1.2$, $p = 0.23$).

4. DISCUSSION

EBS beluga whales consumed energy-dense prey, and primarily Arctic cod from 2011 to 2014. Our QFASA diet estimates are in accordance with our correspondence analysis, and consistent with previ-

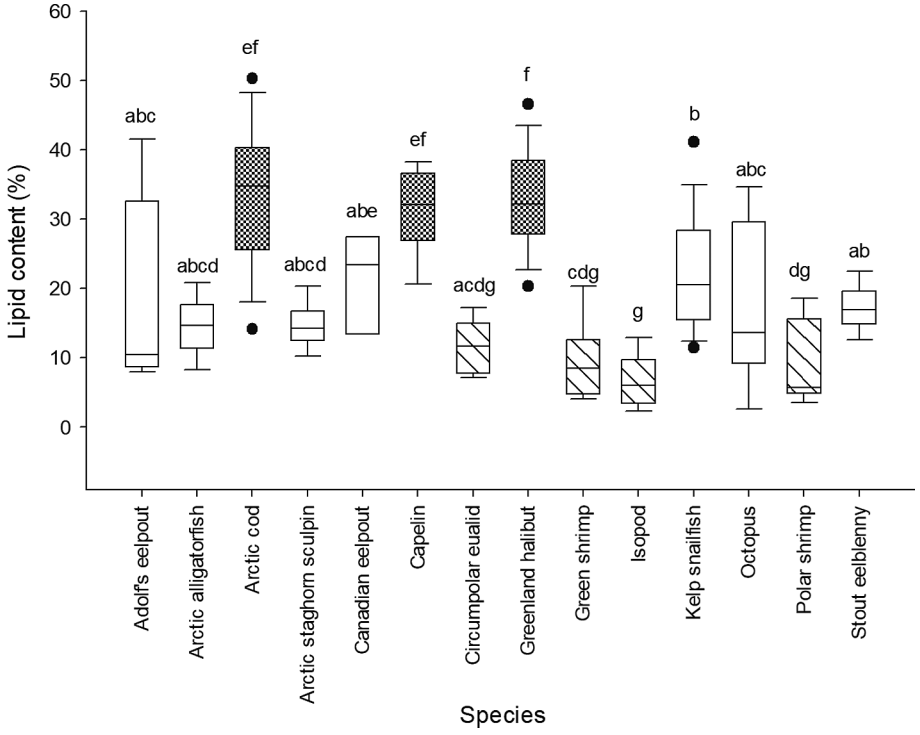

Fig. 4. Percentage lipid content (% of dry weight) of potential prey species of Beaufort Sea beluga whales. Boxes with the same letters are not statistically different (at $\alpha = 0.05$) according to a Tukey HSD test. To highlight significant differences between species groups, boxplots for Arctic cod, Greenland halibut, and capelin are checkered and benthic invertebrates are striped. The lower boundary of the box indicates the 25th percentile, the line within is the median, and the upper boundary indicates the 75th percentile. Error bars define 10th and 90th percentiles. Black dots represent the 5 and 95% percentiles

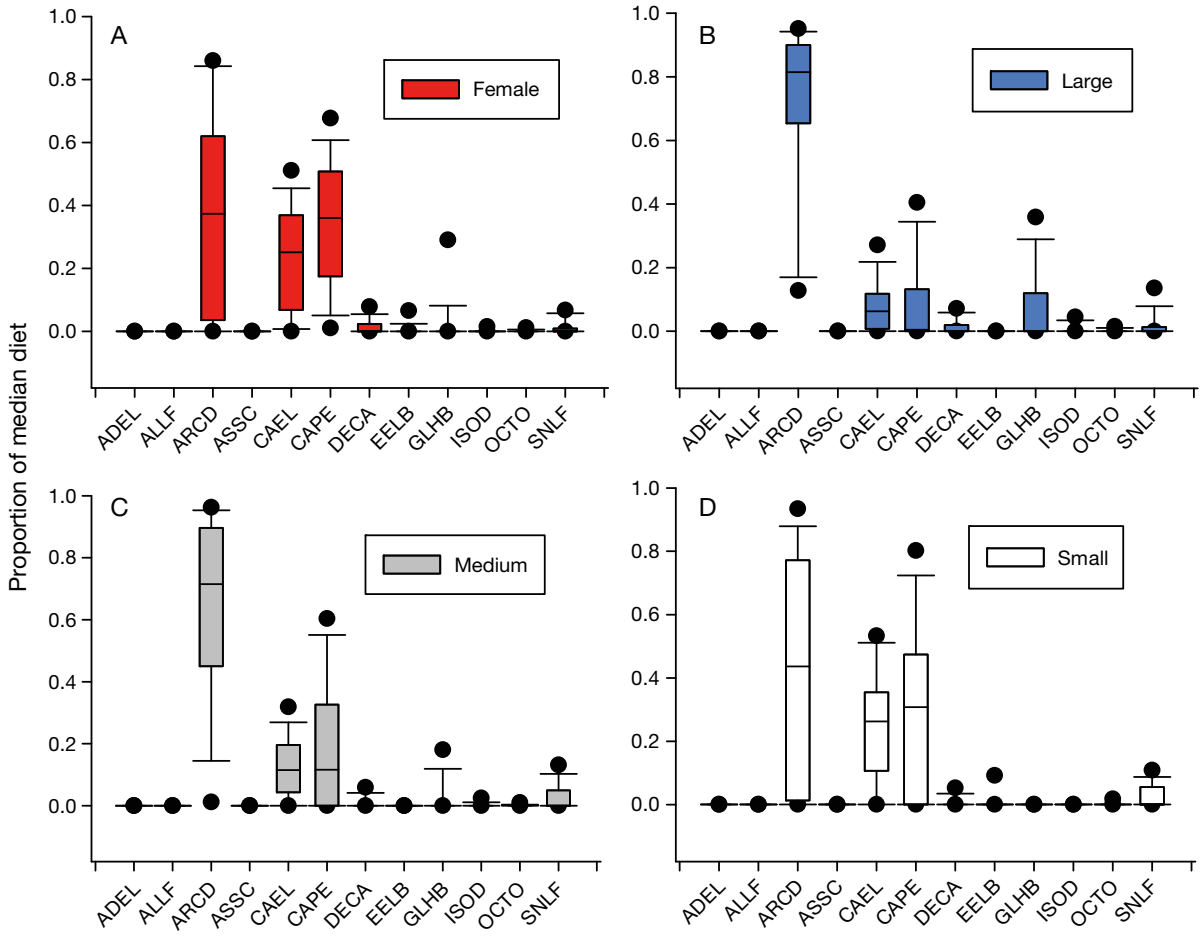

Fig. 5. Median estimates of diet composition for 178 adult Beaufort Sea beluga whales based on different sex and size classes using 25 fatty acid signatures: (A) females, (B) large males (>4.2 m), (C) medium-sized males (3.8–4.2 m), (D) small males (<3.8 m). ADEL: Adolf's eelpout, ALLF: Arctic alligatorfish, ARCD: Arctic cod, ASSC: Arctic staghorn sculpin, CAEL: Canadian eelpout, CAPE: capelin, DECA: decapods, EELB: stout eelblenny, GLHB: Greenland halibut, ISOD: isopod, OCTO: octopus, SNLF: kelp snailfish. The lower boundary of the box indicates the 25th percentile, the line within is the median, and the upper boundary indicates the 75th percentile. Error bars define 10th and 90th percentiles. Black dots represent the 5 and 95% percentiles

ous fatty acid and stomach content analyses of EBS beluga whales (Loseto et al. 2009, Quakenbush et al. 2015). Quakenbush et al. (2015) found Arctic cod to be the predominant prey fish of the EBS beluga population, accounting for 82% of all fish species consumed by whales based on stomach contents collected over a 20 yr period during their spring migration at Point Hope and Little Diomede, Alaska (USA). Arctic cod, capelin, and Greenland halibut had the highest levels of *Calanus* fatty acid markers, the predominant fatty acid signatures in the inner blubber of beluga whales in the present study. *Calanus* copepods, which are consumed by cod and capelin, convert low-energy carbohydrates and proteins produced by phytoplankton and ice algae to high-energy wax esters such as 20:1 and 22:1 fatty alcohols and acids, with the energy content of lipids maximized by increasing chain length (Falk-Petersen et al. 2009).

The difference in $\delta^{15}N$ values between beluga whales and Arctic cod was within the expected range based on trophic discrimination factors of liver from captive studies of other odontocetes (killer whale *Orcinus orca* liver: 2.78‰; Caut et al. 2011), suggesting they are a potential prey. However, the $\delta^{13}C$ values of cod were approximately 3‰ lower than belugas, which was a greater difference than expected based on the trophic discrimination factors of cetacean livers (Caut et al. 2011, Borrell et al. 2012). These results suggest that the carbon source of Arctic cod differed from beluga whales and, therefore, belugas did not consume cod. Stable C and N isotope ratios of Arctic cod in the Canadian Beaufort vary with body size and depth, with larger cod collected from the lower slope (750–1000 m, mean $\delta^{15}N$, $\delta^{13}C$: 14.57, –23.41‰, respectively) having higher $\delta^{15}N$ and $\delta^{13}C$ values than smaller cod from the nearshore

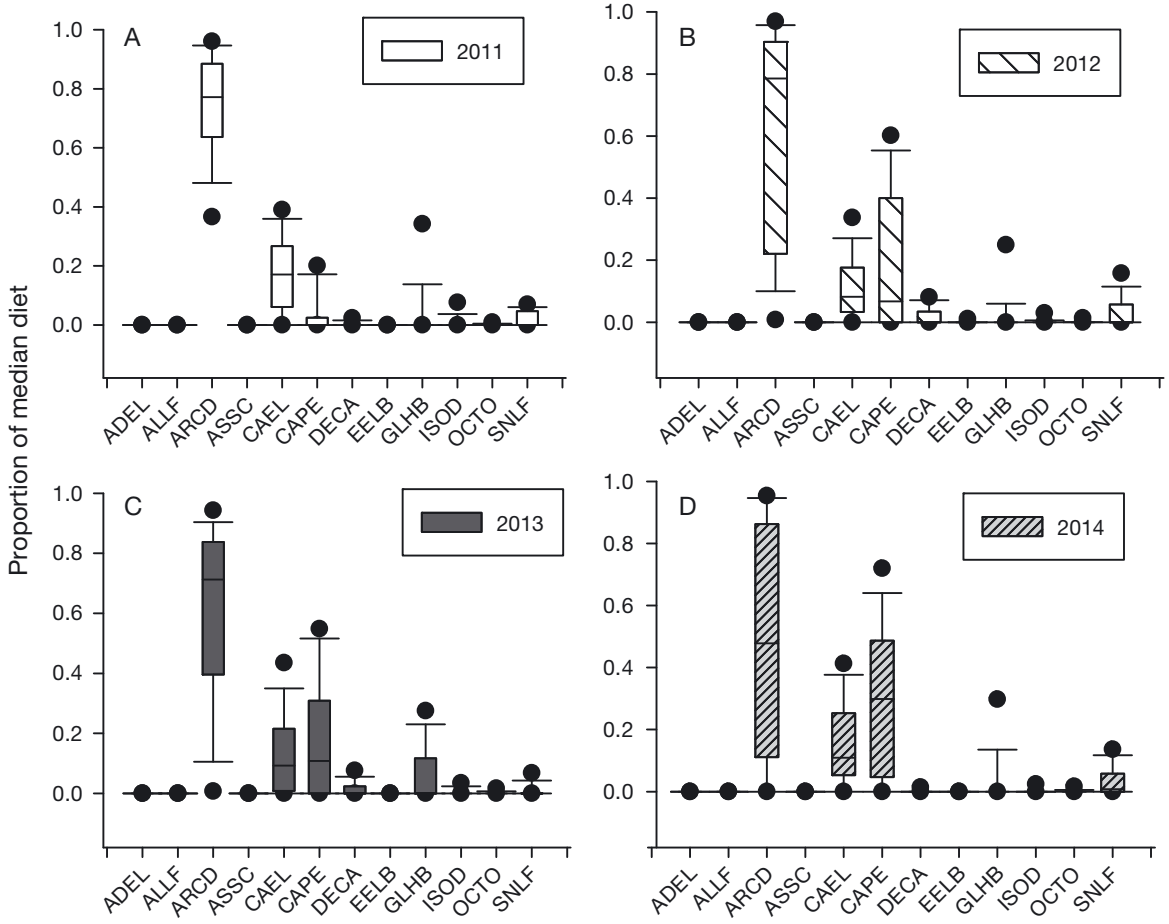

Fig. 6. Median estimates of diet composition for 178 adult Beaufort Sea beluga whales from 2011 to 2014 using 25 fatty acid signatures (prey abbreviations as in Fig. 5). The lower boundary of the box indicates the 25th percentile, the line within is the median, and the upper boundary indicates the 75th percentile. Error bars define 10th and 90th percentiles. Black dots represent the 5 and 95% percentiles

shelf (18–50 m; 12.57, −24.04‰, respectively; Stasko et al. 2016). The differences in locations and depths between the sampling programmes for whales and fish may have caused a mismatch in $\delta^{13}C$ values between prey and predator. In addition, as the belugas had recently migrated, it is possible that $\delta^{13}C$ values of liver still reflected Arctic cod consumed in the Alaskan Bering Sea (mean $\delta^{13}C$ = −20.3‰; Hoekstra et al. 2002), which are higher relative to cod from the Canadian Beaufort Sea (Loseto et al. 2008a, mean = −22.0‰; Stasko et al. 2016, mean range = −24.0 to −23.4‰). In contrast, $\delta^{15}N$ values of cod from the Being Sea (mean = 13.7‰, Hoekstra et al. 2002) and Canadian Beaufort Sea (range: 12.6 to 14.7‰, Loseto et al. 2008b, Stasko et al. 2016) are relatively similar.

While we were unable to acquire prey for all years of our sampled belugas, there was low variability in stable isotope ratios between prey sampled in 2012 and 2013 from the same locations (mean difference <1‰; Stasko et al. 2017). Greenland halibut also demonstrated low variability in fatty acid signatures and stable isotope ratios across years (2012 to 2014) and different sampling depths (Giraldo et al. 2018). Similarly, Arctic cod collected from shelf (15–220 m), upper slope (>220–510 m), and lower slope (>510–800 m) habitats did not vary in fatty acid signatures (Brewster et al. 2018). However, 35.6% of all fatty acids of beluga whales were outside of the mean prey proportions, which may have been caused by inaccuracies in our calibration coefficients (Bromaghin et al. 2015). Calibration coefficients derived from mink feeding trials were poor matches for 20:1n-11 and 22 PUFAs in comparison to estimated calibration coefficients for polar bears, possibly due to differences in physiology (Bromaghin et al. 2017). Chain shortening of 22:1n-11 through metabolism resulted in elevated levels of 18:1 in mink (Cooper et al. 2006), and perhaps differences in the physiology of mink and beluga may also have led to mismatches in 22:1n-11 between beluga whales and their prey.

Without in-depth studies on fatty acid metabolism in whales, this assertion remains untested. Another potential violation of the assumptions of the QFASA model is that beluga whales may have consumed prey species that were not represented in the prey library. As our main finding, which is that Arctic cod is a dominant prey item for EBS beluga whales, is consistent with previous diet analyses (Loseto et al. 2009, Quakenbush et al. 2015), we hypothesize that possibly a minor prey item may not have been included. Improvements to distance metrics have made QFASA more robust to assumption violations, with Aitchison distance measures being the most robust to errors in calibration coefficients (Bromaghin et al. 2015, 2016b). Fat content in several Arctic fish and invertebrate species can also vary with season (Mårtensson et al. 1996), which can affect the digestibility and transfer of fatty acids to predators, leading to errors in approximating the relative proportional contributions of prey (Kirsch et al. 2000, Trumble & Castellini 2005).

Prey estimates varied with the sex and size class, which is in accordance with observed differences in habitat use of the EBS beluga whale population (Loseto et al. 2006) and consistent with previous stomach contents of EBS belugas, which revealed high variability among individuals (Quakenbush et al. 2015). Large males had the highest proportion of Arctic cod and Greenland halibut relative to other sex and size classes. Large males select offshore habitat and are able to access prey at depths beyond 500 m (Martin et al. 2001, Loseto et al. 2006), where large Arctic cod and Greenland halibut are located (Geoffroy et al. 2016, Majewski et al. 2017). Females and small males had higher proportions of capelin and the lowest proportions of cod relative to large and medium-sized males. While Arctic cod occurred in all habitats, transects, and station depths sampled by the BREA MFP survey (Majewski et al. 2016b), the range and habitats used by capelin were more restricted. Capelin were captured in the Amundsen Gulf and Darnley Bay and primarily reside along coastal and shelf areas of the Canadian Beaufort Sea (Majewski et al. 2016a, McNicholl et al. 2016), likely differentially overlapping with the habitat areas used by females and small male belugas, which select coastal and open-water habitat in the Amundsen Gulf (Loseto et al. 2006).

Prey estimates varied among years, with beluga whale consumption of Arctic cod lowest in 2014, which is consistent with fish biomass surveys in the Canadian Beaufort Sea. From 2010 to 2014, hydroacoustic analysis and verified trawl sampling found that the relative abundance and biomass of Arctic cod in the Canadian Beaufort Sea was lower in 2014 in comparison to 2012 or 2013 (Geoffroy 2016, Majewski et al. 2016a), specifically for age-2+ cod from the mesopelagic layer (Geoffroy 2016). Hydroacoustic sampling was focussed in certain areas; therefore, it is unclear whether the lower biomass of Arctic cod in 2014 was the result of: (1) a real decline in absolute abundance, (2) an apparent decline in use of key habitats because the large cod moved elsewhere, or (3) an apparent decline because of cod population dynamics (i.e. a 3 yr life cycle with low abundances of large 3 yr old cod but large abundances of smaller younger cod in other habitats). Although there is a hunter sampling bias towards large males and the usage of offshore ice habitat by larger Arctic cod may be more obvious during years of low cod abundance, we do not believe this is a factor affecting annual variation in diet estimates due to the absence of an interaction effect between year and size class.

According to SIMPER, most of the differences among prey contributions in years and sex and size class were driven by Arctic cod and capelin. Interestingly, the decrease in Arctic cod in beluga diet coincided with an increase in proportions of capelin from 2011 to 2014. With increasing ocean temperatures, capelin has become a more important prey to many marine predators from other Arctic regions. Due to the 'Atlantification' of Hudson Bay, the diet of thick-billed murres *Uria lomvia* has switched from >50% Arctic cod to >50% capelin in the last few decades (Gaston et al. 2003). Beluga whales in Cumberland Sound (Marcoux et al. 2012, Watt et al. 2016, Yurkowski et al. 2018) and Hudson Bay (Kelley et al. 2010) have also increased their capelin consumption over time, hypothesized to result in an energy deficit due to the smaller size of capelin relative to Arctic cod (Watt et al. 2016). Geoffroy (2016) reported that the biomass of Arctic cod in 2014 in the areas sampled in the Canadian Beaufort Sea were insufficient to sustain the energetic requirements of ringed seals *Pusa hispida* and beluga whales. Notably, EBS beluga whales had the lowest body indices in 2014 (Choy et al. 2017), possibly due to the low availability of Arctic cod and/or a greater reliance on capelin, resulting in a lower net energy gain. Other predators in the Beaufort Sea that primarily consume Arctic cod, such as ringed seal and black guillemot *Cepphus grylle* chicks, have also experienced declines in body condition in the past few decades (Harwood et al. 2015). While both species have similar energy densities (Mårtensson et al. 1996, Renkawitz et al. 2015, this study), prey switches from Arctic cod to capelin were believed to be partly responsible for lower nestling growth rates in thick-billed murres

due to the lower body mass of capelin relative to cod and therefore, lower net energy gain (Gaston et al. 2005). Although beluga whales could offset the lower body mass of capelin relative to cod by consuming greater quantities, declines in Arctic cod abundances may not be offset by an increase in capelin as observed in the Bering and Chukchi Seas (De Robertis et al. 2017), since capelin has been reported in Darnley Bay since the 1960s and there is no evidence that the population is increasing (McNicholl et al. 2017). Because our study was conducted over a short time frame, it is difficult to gauge the long-term effects of a prey switch from Arctic cod to capelin in EBS beluga whales. Stock collapses of capelin in the Barents Sea have impacted the body condition, distribution, and reproductive success of various marine mammal, seabird, and fish predators (Gjøsæter et al. 2009); however, the severity of impact of capelin stock collapses on predators depended on the availability of alternative prey sources. It is notable that in 2014, EBS beluga whales were harvested near the communities of Ulukhaktok and Sach Harbour, Northwest Territories, for the first time on record, and sandlance (*Ammodytes* sp.) was the dominant prey species found in 92% of stomachs of these beluga whales (Loseto et al. 2018). Therefore, alternative prey species such as sandlance may also be important in addition to capelin during low cod years.

5. CONCLUSIONS AND FUTURE IMPLICATIONS

In the Canadian Beaufort Sea, beluga whales primarily consumed Arctic cod and other pelagic lipid-rich fish species. Beluga consumed the highest proportions of capelin and the lowest proportions of cod in 2014, the same year in which 2 body condition indices were lowest in all beluga whales (Choy et al. 2017). While our study was conducted over a short period and we cannot directly test for causality or control for other factors, based on the prey switches observed in other Arctic beluga whale populations (Kelley et al. 2010, Yurkowski et al. 2018), future research should examine whether a predominately capelin-based diet may result in declines in energy consumption and condition of beluga whales. Female, calf, and juvenile whales, which primarily use coastal areas, may be most affected since they consume the highest proportions of capelin. Declines in body condition have been associated with decreases in physiological parameters of oxygen stores, possibly affecting foraging ability in EBS beluga whales (Choy et al. 2019a). Therefore, although capelin may provide the same energy density as Arctic cod, population cyclicity and smaller body mass may make capelin a lower-quality food source to beluga whales and other marine predators in the Beaufort Sea ecosystem. Long-term monitoring of beluga diet will help us better predict how whales will respond in the future to changing Arctic conditions. In particular, the long-term effects of beluga whales shifting from an Arctic cod to a capelin-dominated diet should be a priority for monitoring the health and resilience of this population.

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LITERATURE CITED

Allen BM, Angliss RP (2015) Alaska marine mammal stock assessments, 2014. U.S. Dep. Commer., NOAA Tech Memo NMFS-AFSC-301

Anderson MJ, Walsh DCI (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecol Monogr 83:557–574

Anderson M, Gorley RN, Clarke KR (2008) PERMANOVA + for PRIMER: guide to software and statistical methods. PRIMER-E Ltd, Plymouth

Beck MW (2017) Ggord: ordination plots with ggplot2. https://zenodo.org/badge/latestdoi/35334615

Beck CA, Iverson SJ, Bowen WD, Blanchard W (2007) Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. J Anim Ecol 76:490–502

Benoit D, Simard Y, Fortier L (2008) Hydroacoustic detection of large winter aggregations of Arctic cod (*Boreogadus saida*) at depth in ice-covered Franklin Bay (Beaufort Sea). J Geophys Res 113:C06S90

Borrell A, Abad-Oliva N, Gómez-Campos E, Giménez J, Aguilar A (2012) Discrimination of stable isotopes in fin whale tissues and application to diet assessment in cetaceans. Rapid Commun Mass Spectrom 26:1596–1602

Brewster J, Giraldo C, Choy ES, MacPhee SA and others (2018) A comparison of the trophic ecology of Beaufort Sea Gadidae using fatty acids and stable isotopes. Polar Biol 41:149–162

Bromaghin JF (2017a) QFASAR: quantitative fatty acid signature analysis in R. R package version 1.2.0. https://cran.r-project.org/package=qfasar

Bromaghin JF (2017b) QFASAR: quantitative fatty acid signature analysis with R. Methods Ecol Evol 8:1158–1162

Bromaghin JF, Lance MM, Elliott EW, Jeffries SJ, Acevedo-Gutiérrez A, Kennish JM (2013) New insights into the diets of harbor seals (*Phoca vitulina*) in the Salish Sea revealed by analysis of fatty acid signatures. Fish Bull 111:13–26

Bromaghin JF, Rode KD, Budge SM, Thiemann GW (2015) Distance measures and optimization spaces in quantitative fatty acid signature analysis. Ecol Evol 5:1249–1262

Bromaghin JF, Budge SM, Thiemann GW (2016a) Should fatty acid signature proportions sum to 1 for diet estimation? Ecol Res 31:597–606

Bromaghin JF, Budge SM, Thiemann GW, Rode KD (2016b) Assessing the robustness of quantitative fatty acid signature analysis to assumption violations. Methods Ecol Evol 7:51–59

Bromaghin JF, Budge SM, Thiemann GW, Rode KD (2017) Simultaneous estimation of diet composition and calibration coefficients with fatty acid signature data. Ecol Evol 7:6103–6113

Budge SM, Cooper MH, Iverson SJ (2004) Demonstration of the deposition and modification of dietary fatty acids in pinniped blubber using radiolabelled precursors. Physiol Biochem Zool 77:682–687

Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Mar Mamm Sci 22:759–801

Caut S, Laran S, Garcia-Hartmann E, Das K (2011) Stable isotopes of captive cetaceans (killer whales and bottlenose dolphins). J Exp Biol 214:538–545

Chessel D, Dufour AB, Thioulouse J (2004) The ade4 package. I. One-table methods. R News 4:5–10

Choy ES, Roth JD, Loseto LL (2016) Lipid removal and acidification affect nitrogen and carbon stable isotope ratios of beluga whales and their potential prey species in the Beaufort Sea ecosystem. Mar Biol 163:1–13

Choy ES, Rosenberg B, Roth JD, Loseto LL (2017) Interannual variation in environmental factors affect the prey and body condition of beluga whales in the eastern Beaufort Sea. Mar Ecol Prog Ser 579:213–225

Choy ES, Campbell KL, Berenbrink M, Roth JD, Loseto LL (2019a) Body condition impacts blood and muscle oxygen storage capacity of free-living beluga whales (*Delphinapterus leucas*). J Exp Biol 222:jeb191916

Choy ES, Sheehan B, Haulena M, Rosenberg B, Roth JD, Loseto LL (2019b) A comparison of diet estimates of captive beluga whales using fatty acid mixing models with their true diets. J Exp Mar Biol Ecol 516:132–139

Clarke KR, Gorley RN (2015) Primer v7: user manual/tutorial. PRIMER-E Ltd, Plymouth

Clarke KR, Gorley RN, Somerfield PJ, Warwick RM (2014) Change in marine communities: an approach to statistical analysis and interpretation, 3rd edn. PRIMER-E Ltd, Plymouth

Cooper MH, Iverson SJ, Rouvinen-Watt K (2006) Metabolism of dietary cetoleic acid (22:1n-11) in mink (*Mustela vison*) and gray seals (*Halichoerus grypus*) studied using radiolabeled fatty acids. Physiol Biochem Zool 79:820–829

Craig H (1957) Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. Geochim Cosmochim Acta 12: 133–149

De Robertis A, Taylor K, Wilson CD, Farley EV (2017) Abundance and distribution of Arctic cod (*Boreogadus saida*) and other pelagic fishes over the U.S. Continental Shelf of the Northern Bering and Chukchi Seas. Deep Sea Res Part II Top Stud Oceanogr 135:51–65

Falk-Petersen S, Haug T, Nilssen KT, Wold A, Dahl TM (2004) Lipids and trophic linkages in harp seal (*Phoca groenlandica*) from the eastern Barents Sea. Polar Res 23:43–50

Falk-Petersen S, Mayzaud P, Kattner G, Sargent JR (2009) Lipids and life strategy of Arctic *Calanus.* Mar Biol Res 5: 18–39

Folch J, Lees M, Stanley GHS (1957) A simple method for the isolation and purification of total lipids from animal tissues. J Biol Chem 226:497–509

Gaston AJ, Woo K, Hipfner JM (2003) Trends in forage fish populations in northern Hudson Bay since 1981, as determined from the diet of nestling thick-billed murres *Uria lomvia.* Arctic 56:227–233

Gaston AJ, Gilchrist HG, Hipfner JM (2005) Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brunnich's guillemot (*Uria lomvia* L.). J Anim Ecol 74:832–841

Geoffroy M (2016) Signature bioacoustique, distribution et abondance des poissons pélagiques et des mammifères marins en mer de Beaufort (Arctique canadien): une réponse à l'énigme de la morue arctique manquante. PhD thesis, Laval University, Quebec City

Geoffroy M, Robert D, Darnis G, Fortier L (2011) The aggregation of polar cod (*Boreogadus saida*) in the deep Atlantic layer of ice-covered Amundsen Gulf (Beaufort Sea) in winter. Polar Biol 34:1959–1971

Geoffroy M, Majewski A, LeBlanc M, Gauthier S, Walkusz W, Reist JD, Fortier L (2016) Vertical segregation of age-0 and age-1+ polar cod (*Boreogadus saida*) over the annual cycle in the Canadian Beaufort Sea. Polar Biol 39: 1023–1037

Giraldo C, Stasko A, Choy ES, Rosenberg B and others (2016) Trophic variability of Arctic fishes in the Canadian Beaufort Sea: a fatty acids and stable isotopes approach. Polar Biol 39:1267–1282

Giraldo C, Stasko A, Walkusz W, Majewski A and others (2018) Feeding of Greenland halibut (*Reinhardtius hippoglossoides*) in the Canadian Beaufort Sea. J Mar Syst 183:32–41

Gjøsæter H, Bogstad B, Tjelmeland S (2009) Ecosystem effects of the three capelin stock collapses in the Barents Sea. Mar Biol Res 5:40–53

Goetsch C, Conners MG, Budge SM, Mitani Y and others (2018) Energy-rich mesopelagic fishes revealed as a critical prey resource for a deep-diving predator using quantitative fatty acid signature analysis. Front Mar Sci 5:1–19

Greenacre M, Primicerio R (2013) Multivariate analysis of ecological data. Fundacion BBVA, Bilbao

Harter BB, Elliott KH, Divoky GJ, Davoren GK (2013) Arctic cod (*Boreogadus saida*) as prey: fish length–energetics relationships in the Beaufort Sea and Hudson Bay. Arctic 66:191–196

Harwood LA, Smith TG (2002) Whales of the Inuvialuit settlement region in Canada's Western Arctic: an overview and outlook. Arctic 55:77–93

Harwood LA, Kingsley MCS, Smith TG (2014) An emerging pattern of declining growth rates in belugas of the Beaufort Sea: 1989–2008. Arctic 67:483–492

Harwood LA, Smith TG, George JC, Sandstrom SJ, Walkusz W, Divoky GJ (2015) Change in the Beaufort Sea ecosystem: diverging trends in body condition and/or production in five marine vertebrate species. Prog Oceanogr 136:263–273

Hoekstra PF, Dehn LA, George JC, Solomon KR, Muir DCG, 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

Iverson SJ, Field C, Bowen WD, Blanchard W (2004) Quantitative fatty acid signatures analysis: a new method of estimating predator diets. Ecol Monogr 74:211–235

Kelley TC, Loseto LL, Stewart REA, Yurkowski M, Ferguson SH (2010) Importance of eating capelin: unique dietary habits of Hudson Bay beluga. In: Ferguson SH, Loseto LL, Mallory ML (eds) A little less Arctic: top predators in the world's largest northern inland sea, Hudson Bay. Springer, Dordrecht, p 53–70

Kirsch PE, Iverson SJ, Bowen WD (2000) Effect of a low-fat diet on body composition and blubber fatty acids of captive juvenile harp seals (*Phoca groenlandica*). Physiol Biochem Zool 73:45–59

Laidre KL (2008) Background document for development of a circumpolar beluga whale (*Delphinapterus leucas*) monitoring plan. US Marine Mammal Commission, Bethesda, MD

Laidre KL, Stern H, Kovacs KM, Lowry L and others (2015) Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. Conserv Biol 29:724–737

Laurel BJ, Spencer M, Iseri P, Copeman LA (2016) Temperature-dependent growth and behavior of juvenile Arctic cod (*Boreogadus saida*) and co-occurring North Pacific gadids. Polar Biol 39:1127–1135

Lind Y, Bäcklin BM, Lundström K, Budge SM, Walton M, Karlsson O (2012) Stability of fatty acid composition in seal blubber during long-term storage. Mar Ecol Prog Ser 461:283–291

Loseto LL, Richard P, Stern GA, Orr J, Ferguson SH (2006) Segregation of Beaufort Sea beluga whales during the open-water season. Can J Zool 84:1743–1751

Loseto LL, Stern GA, Deibel D, Connelly TL and others (2008a) Linking mercury exposure to habitat and feeding behaviour in Beaufort Sea beluga whales. J Mar Syst 74: 1012–1024

Loseto LL, Stern GA, Ferguson SH (2008b) Size and biomagnification: how habitat selection explains beluga mercury levels. Environ Sci Technol 42:3982–3988

Loseto LL, Stern GA, Connelly TL, Deibel D and others (2009) Summer diet of beluga whales inferred by fatty acid analysis of the eastern Beaufort Sea food web. J Exp Mar Biol Ecol 374:12–18

Loseto LL, Brewster JD, Ostertag SK, Snow K and others (2018) Diet and feeding observations from an unusual beluga harvest in 2014 near Ulukhaktok, Northwest Territories, Canada. Arct Sci 4:421–431

Majewski A, Suchy K, Atchison S, Henry J and others (2016a) Uniqueness of fishes and habitat utilization in oil & gas lease blocks relative to non-lease areas in the Canadian Beaufort Sea. Environmental Studies Research Funds. ESRF Project: 2012-04N. Rep Ser 203. ESRF, Ottawa

Majewski AR, Walkusz W, Lynn BR, Atchison S, Eert J, Reist JD (2016b) Distribution and diet of demersal Arctic Cod, *Boreogadus saida*, in relation to habitat characteristics in the Canadian Beaufort Sea. Polar Biol 39:1087–1098

Majewski AR, Atchison S, MacPhee S, Eert J, Niemi A, Michel C, Reist JD (2017) Marine fish community structure and habitat associations on the Canadian Beaufort shelf and slope. Deep Sea Res Part I Oceanogr Res Pap 121:169–182

Marcoux M, McMeans BC, Fisk AT, Ferguson SH (2012) Composition and temporal variation in the diet of beluga whales, derived from stable isotopes. Mar Ecol Prog Ser 471:283–291

Mariotti A (1983) Atmospheric nitrogen is a reliable standard for natural ^{15}N abundance measurements. Nature 303:685–687

Mårtensson PE, Lager Gotaas AR, Nordøy ES, Blix AS (1996) Seasonal changes in energy density of prey of Northeast Atlantic seals and whales. Mar Mamm Sci 12:635–640

Martin AR, Hall P, Richard PR (2001) Dive behaviour of belugas (*Delphinapterus leucas*) in the shallow waters of western Hudson Bay. Arctic 54:276–283

McNicholl DG, Walkusz W, Davoren GK, Majewski AR, Reist JD (2016) Dietary characteristics of co-occurring polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) in the Canadian Arctic, Darnley Bay. Polar Biol 39: 1099–1108

McNicholl DG, Wolki B, Ostertag SK (2017) Traditional ecological knowledge and local observations of capelin (*Mallotus villosus*) in Darnley Bay, NT. Can Manuscr Rep Fish Aquat Sci 3144:1–20

Moore SE, Huntington HP (2008) Arctic marine mammals and climate change: impacts and resilience. Ecol Appl 18:s157–s165

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

Nordstrom CA, Wilson LJ, Iverson SJ, Tollit DJ (2008) Evaluating quantitative fatty acid signature analysis (QFASA) using harbour seals *Phoca vitulina richardsi* in captive feeding studies. Mar Ecol Prog Ser 360:245–263

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703–718

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

Quakenbush LT, Suydam RS, Bryan AL, Lowry LF, Frost KJ, Mahoney BA (2015) Diet of beluga whales (*Delphinapterus leucas*) in Alaska from stomach contents, March–November. Mar Fish Rev 77:70–84

R Core Team (2018) R: a language and environment for statistical computing. Version 3.4.4. https://www.R-project.org/

Renkawitz MD, Sheehan TF, Dixon HJ, Nygaard R (2015) Changing trophic structure and energy dynamics in the Northwest Atlantic: implications for Atlantic salmon feeding at West Greenland. Mar Ecol Prog Ser 538:197–211

Richard PR, Martin AR, Orr JR (2001) Summer and autumn movements of belugas of the eastern Beaufort Sea stock. Arctic 54:223–236

Seaman GA, Frost KJ, Lowry LF (1982) Foods of belukha whales (*Delphinapterus leucas*) in western Alaska. Cetology 44:1–10

SIMIP Community (2020) Arctic Sea Ice in CMIP6. Geophys Res Lett 47:e2019GL086749

Stasko AD, Swanson H, Majewski A, Atchison S, Reist J, Power M (2016) Influences of depth and pelagic subsidies on the size-based trophic structure of Beaufort Sea fish communities. Mar Ecol Prog Ser 549:153–166

Stasko AD, Swanson H, Atchison S, MacPhee S and others (2017) Stable isotope data ($\delta^{15}N$, $\delta^{13}C$) for marine fishes and invertebrates from the Beaufort Regional Environmental Assessment Marine Fishes Project, August–September 2012 and 2013. Can Data Rep Fish Aquat Sci 1270

Stroeve J, Notz D (2018) Changing state of Arctic sea ice across all seasons. Environ Res Lett 13:103001

Stroeve J, Holland MM, Meier W, Scambos T, Serreze M (2007) Arctic sea ice decline: faster than forecast. Geophys Res Lett 34:L09501

Thiemann GW, Iverson S, Stirling I (2008) Polar bear diets and Arctic marine food webs: insights from fatty acid analysis. Ecol Monogr 78:591–613

Trumble SJ, Castellini MA (2005) Diet mixing in an aquatic carnivore, the harbour seal. Can J Zool 83:851–859

Tynan C, DeMaster DP (1997) Observations and predictions of Arctic climatic change: potential effects on marine mammals. Arctic 50:308–322

Wang M, Overland JE (2012) A sea ice free summer Arctic within 30 years: an update from CMIP5 models. Geophys Res Lett 39:L18501

Watt CA, Orr J, Ferguson SH (2016) A shift in foraging behaviour of beluga whales *Delphinapterus leucas* from the threatened Cumberland Sound population may reflect a changing Arctic food web. Endang Species Res 31:259–270

Welch HE, Bergmann MA, Siferd TD, Martin KA and others (1992) Energy flow through the marine ecosystem of the Lancaster Sound Region, Arctic Canada. Arctic 45: 343–357

Welch HE, Crawford RE, Hop H (1993) Occurrence of Arctic cod (*Boreogadus saida*) and their vulnerability to predation in the Canadian High Arctic. Arctic 46:331–339

Yurkowski DJ, Hussey NE, Ferguson SH, Fisk AT (2018) A temporal shift in trophic diversity among a predator assemblage in a warming Arctic. R Soc Open Sci 5: 180259

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