



Ice-algal carbon supports harp and ringed seal diets in the European Arctic: evidence from fatty acid and stable isotope markers

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ABSTRACT: Sea-ice declines in the European Arctic have led to substantial changes in marine food webs. To better understand the biological implications of these changes, we quantified the contributions of ice-associated and pelagic carbon sources to the diets of Arctic harp and ringed seals using compound-specific stable isotope ratios of fatty acids in specific primary producer biomarkers derived from sea-ice algae and phytoplankton. Comparison of fatty acid patterns between these 2 seal species indicated clear dietary separation, while the compound-specific stable isotope ratios of the same fatty acids showed partial overlap. These findings suggest that harp and ringed seals target different prey sources, yet their prey rely on ice and pelagic primary production in similar ways. From Bayesian stable isotope mixing models, we estimated that relative contributions of sympagic and pelagic carbon in seal blubber was an average of 69 % and 31 % for harp seals, and 72 % and 28 % for ringed seals, respectively. The similarity in the Bayesian estimations also indicates overlapping carbon sourcing by these 2 species. Our findings demonstrate that the seasonal ice-associated carbon pathway contributes substantially to the diets of both harp and ringed seals.

KEY WORDS: Carbon source · Climate change · Food webs · Compound-specific stable isotopes · Foraging · Pinnipeds · Sea-ice algae · Phytoplankton

1. INTRODUCTION

Niche partitioning theory states that species co-existing in the same foraging space are expected to have different diets or resource use, effectively limiting competition (MacArthur 1958). In the European Arctic, harp (*Pagophilus groenlandicus*) and ringed (*Pusa hispida*) seals are found in similar habitats for at least part of the year, along the sea-ice edge and in coastal Svalbard waters during spring and summer (Hamilton et al. 2021). They often target similar ice-

associated prey (Nilssen et al. 1995b, Labansen et al. 2007, Lindstrøm et al. 2013), but exhibit some niche separation via differences in foraging behavior (dive depth, size of prey selected; Wathne et al. 2000). Trophic niche partitioning can be characterized by dietary composition but also by which carbon end members (i.e. autotrophic primary producers) support their prey sources, and both aspects are studied here. In the Arctic specifically, some of the organic carbon of their prey can be traced back to sea-ice primary production (Kohlbach et al. 2017), an early-

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season energy source that fuels food webs within the Arctic (Ji et al. 2013). Arctic sea-ice declines have already resulted in breeding and foraging habitat reductions for harp and ringed seals (Hamilton et al. 2017, 2019, Stenson et al. 2020). These pinnipeds will likely encounter increased competition in the remaining sea-ice areas from boreal species shifting northward (Kovacs et al. 2011, Øigård et al. 2013) and from each other, given that they are increasingly overlapping in some areas of their Barents Sea distributions (Bengtsson et al. 2020). The overall reduction or loss of sea-ice primary production and its cumulative effects on food webs are currently unknown, though harp seals are showing declining body condition that is thought to be due to competition with other predators, including the large standing stock of Atlantic cod *Gadus morhua*, which has shifted northward in the Barents Sea region (Stenson et al. 2020).

Harp and ringed seals are 2 ice-associated seals, but the nature of their dependence on sea ice differs. Both species are monitored in the study region and are harvested for subsistence (harp seals, Greenland) or commercially (ringed seals, Svalbard). Harp seals are a North Atlantic drift-ice breeding species that migrates into the High Arctic for summer feeding (Stenson et al. 2020). They associate with sea ice most of the year but can spend time in open-water areas outside the moulting and breeding seasons; therefore, their diets are particularly variable by season and region (e.g. Nilssen et al. 1995a,b, Lawson & Hobson 2000, Stenson et al. 2020). Harp seals from the Greenland and White Seas perform seasonal migrations from southerly breeding areas, where they use drift or land-fast ice, northward to the sea-ice edge north of Svalbard for summer and autumn foraging (Haug et al. 1994, Folkow et al. 2004). These foraging migrations are important for regaining energy stores used during the breeding and moulting seasons in the spring (Nilssen et al. 1997).

Ringed seals are a circumpolar Arctic species that is highly reliant on sea ice throughout the year (Laidre et al. 2008). Their diet is also known to vary regionally and seasonally (Holst et al. 2001, Thiemann et al. 2007, Bengtsson et al. 2020). In Svalbard, ringed seal movement and diving patterns suggest that adult animals forage primarily at tidewater glacier fronts (Hamilton et al. 2016, 2019) and trends in the recent decade show that they are retracting into these Arctic refugial areas as sea-ice declines continue (Hamilton et al. 2019). Young ringed seals do not stay coastal in summer; they migrate north to the sea-ice edge to forage (Freitas et al. 2008, Hamilton et al. 2015). Despite having to travel longer to reach

the sea ice in recent years, they are still undertaking these foraging migrations (Hamilton et al. 2015).

For many Arctic organisms, sympagic (ice-associated) primary production is an essential early-season energy source (McMahon et al. 2006, Søreide et al. 2010, Ji et al. 2013). This production supports prey of higher trophic levels such as seabirds and walrus *Odobenus rosmarus rosmarus* (Cusset et al. 2019, Yurkowski et al. 2020). In the Eurasian Basin, which is partially covered by sea ice year-round, sympagic carbon contributed as much as 92% to the diets of various under-ice and pelagic zooplankton and between 34 and 65% for various tissues of polar cod *Boreogadus saida* (Kohlbach et al. 2016, 2017). In the seasonally ice-covered Bering Sea, sympagic primary production has also been shown to make high contributions to the diets of ice-associated seals, with estimates ranging from 62 to 80% for bearded seals *Erignathus barbatus*, 21 to 60% for ringed seals, and 51 to 62% for spotted seals *Phoca largha* (Wang et al. 2016). It is unknown whether Arctic seal diets in the European Arctic also have similarly high contributions of sea-ice algal-sourced carbon, as pelagic primary production would be expected to be more important in the seasonal ice-covered zones.

Organic carbon in sea-ice-covered ecosystems originates primarily from ice algae and phytoplankton. These primary producers often have distinct carbon isotope signatures ($\delta^{13}\text{C}$), largely due to the fact that sea-ice algae compete for light and space in a closed carbon-limiting system that has minimal exchange with the underlying water column (Horner & Schrader 1982, Fry & Sherr 1984, Kennedy et al. 2002). As a result, bulk $\delta^{13}\text{C}$ values of ice algae are often higher when compared to phytoplankton values (Gradinger 2009, de la Vega et al. 2019), though these values can overlap with one another depending on ice algal biomass and the time of year when sampling takes place (Søreide et al. 2006, Tremblay et al. 2006, Gradinger 2009). Bulk stable isotope analysis of carbon is most widely used (de la Vega et al. 2019), but delivers a single value encompassing a mixture of all organic compounds. In contrast, compound-specific stable isotope analysis provides more detailed information on the sources of individual compounds, such as fatty acids, which in themselves can be used as tracers in food web studies (Middelburg 2014, Burian et al. 2020).

Complementary to isotopic research, the trophic biomarker approach is a selective process involving certain marker fatty acids that can be used to determine consumer diets and energy flow within food webs (Lee et al. 1971, Sargent & Whittle 1981, Falk-

Petersen et al. 1990). Two of the most abundant fatty acids in Bacillariophyceae, or diatoms, are 16:1(n-7) and 20:5(n-3) (Viso & Marty 1993, Reitan et al. 1994, Jónasdóttir 2019). Sea ice in general and specifically first-year sea-ice algal communities are often dominated by diatoms (Leu et al. 2006, Søreide et al. 2006, Fernández-Méndez et al. 2018), which contribute the highest algal fraction to sea-ice particulate organic matter (Van Leeuwe et al. 2018). Dinoflagellates (Dinophyceae) also have characteristic marker fatty acids, namely, higher amounts of 18:4(n-3) and 22:6(n-3) (Viso & Marty 1993, Graeve et al. 1994). These fatty acids are characteristic for diatoms or dinoflagellates occurring in sea ice and/or water (Søreide et al. 2008), but again these specific fatty acids in particulate organic matter inside sea ice can have higher $\delta^{13}\text{C}$ values (Wang et al. 2014). Thus, combining marker fatty acids with their individual stable isotope values, or $\delta^{13}\text{C}_{\text{FA}}$, may provide further differentiation between carbon sources and their assimilation pathways throughout food webs (Budge et al. 2008).

The overarching objective in this study was to identify potential trophic niche differences between harp and ringed seals from 2 angles: firstly, by identifying potential differences in dietary items (fatty acid analysis), and secondly, by identifying potential differences in carbon sourcing from phytoplankton and ice algae (isotopic ratio analysis). To address these 2 aspects, we used fatty acids and $\delta^{13}\text{C}_{\text{FA}}$ to (1) determine any differences in sea-ice algae and phytoplankton values, (2) evaluate potential dietary fatty acid compositional differences between harp and ringed seals, and (3) estimate the relative contribution of sympagic and pelagic primary production to harp and ringed seal diets using the $\delta^{13}\text{C}_{\text{FA}}$ values of 4 trophic biomarker fatty acids. Based on previous studies documenting differences in $\delta^{13}\text{C}_{\text{FA}}$ values in ice algae and phytoplankton (Budge et al. 2008, Wang et al. 2014), we first predicted that even if the fatty acid compositions of the 2 primary production sources were similar, sympagic algae would have $\delta^{13}\text{C}_{\text{FA}}$ values higher than pelagic values. Second, we hypothesized that fatty acid profiles would be similar between the 2 seal species given their dietary overlap. Third, we hypothesized that sympagic carbon is more likely to contribute to the diet of ringed seals because of their stronger association with sea ice.

2. MATERIALS AND METHODS

To address our first hypothesis, we examined the fatty acid compositions and specific $\delta^{13}\text{C}_{\text{FA}}$ values of

sea-ice algae and phytoplankton in summer and determined if there were differences between the 2 sources of primary production. To address hypothesis 2, we tested if harp and ringed seals differed in their blubber fatty acid compositions and the $\delta^{13}\text{C}_{\text{FA}}$ values of the trophic biomarker fatty acids. Finally, to address hypothesis 3, differences in the $\delta^{13}\text{C}_{\text{FA}}$ values between sympagic and pelagic sources were used to quantify the contribution of these different carbon sources to the harp and ringed seal diets.

2.1. Study area and sample collection

Sea-ice algae and phytoplankton were collected north of Svalbard, over the Yermak Plateau, in the northern Barents Sea and in the Nansen Basin (Fig. 1). Sample collection of particulate organic matter from sea-ice algae and phytoplankton occurred during 2 consecutive cruises onboard the RV 'Polarstern' (Fig. 1). From 3 to 15 June 2017, the RV 'Polarstern' was anchored to an ice floe north of Svalbard. During this time, the ice floe drifted approximately 100 km, circling above the Yermak Plateau (Fig. 1). From 25 June to 14 July, the RV 'Polarstern' traveled north through the Barents Sea and into the deep Nansen Basin. Sample collection occurred at various stations throughout this area (Table 1). In-ice chlorophyll *a* ranged from 0.11 to 0.39 mg m⁻² (Castellani et al. 2020), and all sea ice encountered during both cruises was first-year ice.

Particulate organic matter within sea ice (iPOM) was collected by taking ice cores with a 9 cm inner diameter ice corer (Kovacs Enterprises). The bottom 5 cm of each ice core was cut off and melted onboard the ship in a 4°C dark room. To obtain more material, ice-algae aggregates floating in auger holes were opportunistically collected by hand and placed into 50 ml Falcon tubes (Fisher Scientific). During 3–15 June, iPOM was collected from 7 ice cores and 4 floating ice-algae aggregates. During 25 June–14 July, iPOM was collected from 17 ice cores taken at 5 ice stations and 6 hand-collected ice-algae aggregates were collected at 3 ice stations. Particulate organic matter from the phytoplankton community (pPOM) was also collected during both cruises. During 3–15 June, only one pPOM water sample (at 30 m) ended up being usable and was taken by hand through a hole in the sea ice using a Kemmerer water sampler (Eijkelpamp). During 25 June–14 July, pPOM was collected at 12 different stations using a CTD rosette water sampler (Seabird SBE9+) at the chlorophyll maximum layer (between 6 and 40 m). All samples

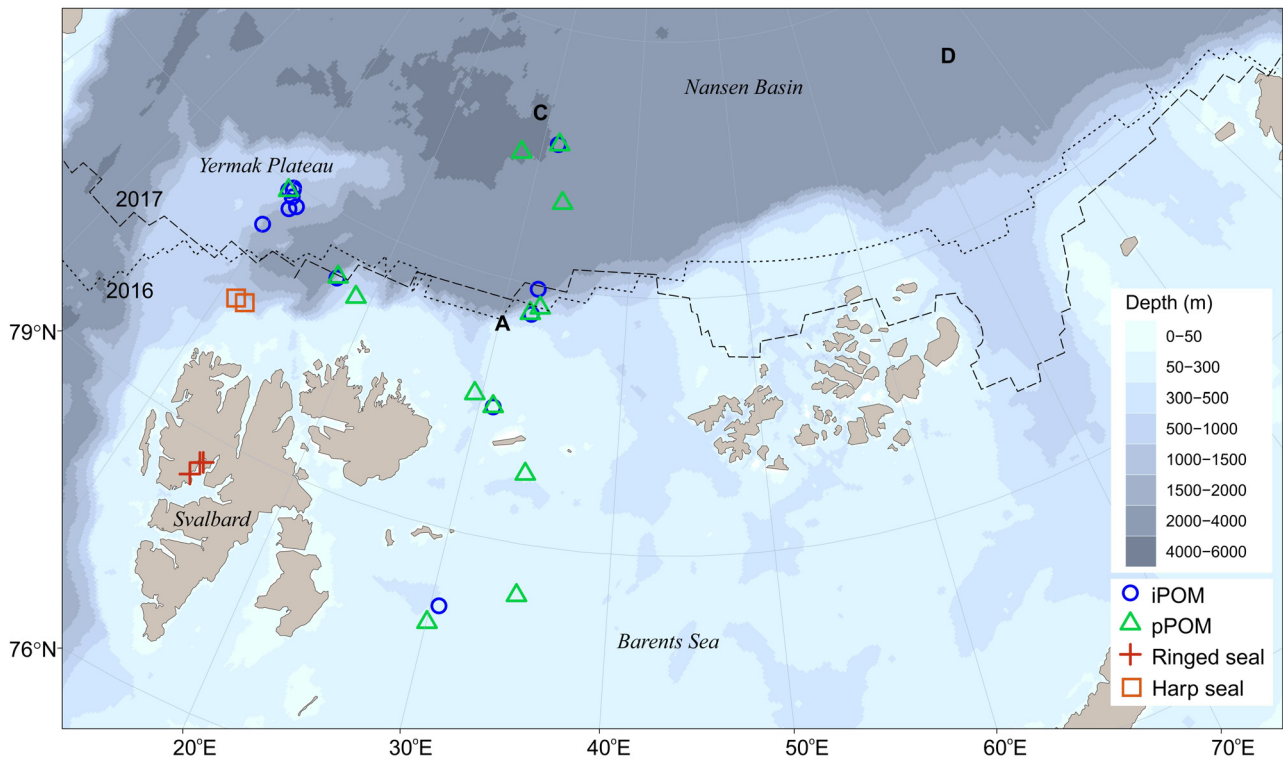


Fig. 1. Map of the study area. Black lines show minimum September sea-ice extent in 2016 (dotted line) and 2017 (dashed line; data: National Snow and Ice Data Center, Fetterer et al. [2017]). A, C, and D refer to pPOM stations included from Kohlbach et al. (2017). The study area map was generated with the ggOceanMaps package (Vihtakari 2020)

were filtered onto 0.7 μm pre-combusted GF/F filters (Whatman, Merck). Filtered samples were subsequently wrapped in aluminum foil and stored in a -80°C freezer until analysis.

Harp seals ($n = 25$) were shot for scientific purposes on ice floes north of Svalbard (80.52° – 80.55° N, 11.4° – 11.8° E), and samples were collected on 11 September 2016 (Fig. 1). Ringed seals were shot ($n = 20$) during an annual sport hunt that occurs in Svalbard each summer and autumn. Ringed seal samples were collected in Eckmanfjorden (78.49 – 78.66° N, 14.40 – 14.58° E), Svalbard, between 26 June and 21 September 2017 (Fig. 1). Seal age was determined by counting cementum layers of sectioned teeth (mostly canines) (Scheffer 1950). For both species, ages <1 yr were considered young of the year, ages 1–5 yr as juveniles, and seals ≥ 6 yr as adults (Lydersen & Gjertz 1987). Full-depth (from skin to muscle) blubber samples were taken from the trunk of the seal bodies immediately after collection, wrapped in aluminum foil and frozen at -20°C until arrival at the laboratory, where they were subsequently stored at -80°C until analysis. Blubber tissue fatty acids reflect signatures of acquired prey items consumed over time periods from weeks to months in seals (Nordstrom et al. 2008, Tollit

et al. 2010). While different sections of blubber can reflect different time periods of when prey was acquired (Strandberg et al. 2008), we were interested in the cumulative incorporation of diet and carbon sources, and hence homogenized the whole blubber column.

2.2. Fatty acid analysis

All laboratory analyses were conducted at the Alfred Wegener Institute in Bremerhaven, Germany. Prior to lipid extraction, POM samples were removed from -80°C freezers and freeze-dried for 24 h. Seal blubber was first thawed in a refrigerator, and a longitudinal slice (from skin to muscle) was cut using a clean scalpel on a glass plate. The skin and any attached muscle tissue were cut away, and one blubber sample was analyzed per individual. Blubber samples were placed on individual pieces of aluminum foil and freeze-dried for 24 h (Rudy et al. 2016) leaving 2–9 g (dry mass) of blubber per individual.

Samples were mechanically homogenized, and lipids were extracted using dichloromethane/methanol 2:1 v/v (Folch et al. 1957). Total lipid mass of each sample was determined gravimetrically. Lipids were

Table 1. Sample information for particulate organic matter from sea ice (iPOM) and phytoplankton (pPOM) collected from the Yermak Plateau (PS106.1), Barents Sea (PS106.2), and Nansen Basin (PS106.2), and for harp and ringed seals. Samples were analyzed for fatty acids (FA) and carbon isotope values of fatty acids ($\delta^{13}\text{C}_{\text{FA}}$). Sea-ice coverage was acquired from the Copernicus Marine Service (<https://marine.copernicus.eu/>), which provides daily ice cover by 10 km² for pack ice (POM and harp seal locations) and 1 km² for land-fast ice (ringed seal locations)

Group	Sample type	Data	N	Date	Latitude (°N)	Longitude (°E)	Station	Sea-ice coverage (%)
POM, PS106.1	iPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	1	2 June 2017	81.411	9.786	19	91
	iPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	1	4 June 2017	81.964	10.243	21	96
	iPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	2	7 June 2017	81.942	10.308	24	95
	iPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	2	9 June 2017	81.909	10.006	26	93
	pPOM	FA only	1	9 June 2017	81.909	10.006		93
	iPOM	FA only	2	11 June 2017	81.867	10.557	28	99
	iPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	2	14 June 2017	81.798	11.285	31	100
	iPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	1	15 June 2017	81.731	10.858	32	100
POM, PS106.2	pPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	1	25 June 2017	77.894	30.045	44	61
	iPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	7	25 June 2017	78.111	30.479	45	63
	pPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	1	26 June 2017	78.405	34.703	47	28
	pPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	1	27 June 2017	79.815	34.018	48	70
	pPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	1	28 June 2017	80.515	30.972	50	94
	iPOM	FA only	2	29 June 2017	80.508	30.984		86
	pPOM	FA only	1	30 June 2017	81.750	32.938	57	95
	iPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	7	2 July 2017	81.655	32.342	66	98
	pPOM	FA only	1	2 July 2017	81.664	32.237		98
	iPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	2	3 July 2017	81.958	32.482	67	95
	pPOM	FA only	1	5 July 2017	83.000	33.162	69	90
	iPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	3	6 July 2017	83.661	31.581	73	91
	pPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	1	7 July 2017	83.664	31.721		92
	pPOM	FA only	1	8 July 2017	83.473	28.055	74	83
	iPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	2	12 July 2017	81.308	16.886	80	78
	pPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	1	12 July 2017	81.326	16.928		78
	pPOM	$\delta^{13}\text{C}_{\text{FA}}$, FA	1	13 July 2017	81.205	18.835	83	89
pPOM	FA only	1	14 July 2017	80.611	29.489	85	73	
Harp		$\delta^{13}\text{C}_{\text{FA}}$, FA	25	11 Sep 2016	80.517	11.400		4
Ringed		$\delta^{13}\text{C}_{\text{FA}}$, FA	3	26 June 2017	78.491	14.400		20
		$\delta^{13}\text{C}_{\text{FA}}$, FA	6	29 Aug 2017	78.491	14.400		20
		$\delta^{13}\text{C}_{\text{FA}}$, FA	2	9 Sep 2017	78.491	14.400		50
		$\delta^{13}\text{C}_{\text{FA}}$, FA	3	17 Sep 2017	78.664	14.582		5
		$\delta^{13}\text{C}_{\text{FA}}$, FA	6	21 Sep 2017	78.684	14.754		0

then converted into fatty acid methyl esters by using a solution of 3 % concentrated sulfuric acid in methanol and heating for 4 h at 80°C (Kattner & Fricke 1986). Subsequently, fatty acid methyl esters were quantified using an Agilent 6890N gas chromatograph (Agilent Technologies) with a DB-FFAP capillary column (60 m, 0.25 mm i.d., 0.25 μm film thickness) supplied with a splitless injector and a flame ionization detector using temperature programming. Helium was used as the carrier gas. Fatty acid methyl esters were quantified with an internal standard, tricosanoic acid methyl ester (23:0) (Supelco), that was added prior to lipid extraction. The detection limit based on the certified reference material (Supelco 37 Component fatty acid methyl ester mix) was 10–20 ng per component. Clarity chromatography software system (version 8.2.0,

DataApex) was used for chromatogram data evaluation. Fatty acids are presented in shorthand notation, i.e. A:B(n-x), where A indicates the number of carbon atoms in the straight fatty acid chain, B represents the number of double bonds present, n represents the terminal methyl group and x denotes the position of the first double bond from the terminal end. Proportions of fatty acids are expressed as mass percentages of total fatty acid content.

2.3. Compound-specific stable isotope analysis

Carbon stable isotope ratios of fatty acid methyl esters ($\delta^{13}\text{C}_{\text{FA}}$) of both POM and seal samples were analyzed using a Trace Ultra gas chromatograph (GC), a

GC Isolink system, and a Delta V Plus isotope ratio mass spectrometer (IRMS), connected to a Conflo IV interface (Thermo Scientific Corporation). Samples were injected in splitless mode and separated on a DB-FFAP column (60 m, 0.25 mm i.d., 0.25 μ m film thickness) using temperature programming (Kohlbach et al. 2016). The limit of detection was comparable to the methods described above. The $\delta^{13}\text{C}_{\text{FA}}$ values were calibrated using certified standards of 14:0 ($\delta^{13}\text{C}$: -29.98%), 16:0 ($\delta^{13}\text{C}$: -30.74%), 18:0 ($\delta^{13}\text{C}$: -23.24%), and 20:0 ($\delta^{13}\text{C}$: -30.68%) (supplied by Indiana University, USA). To ensure accuracy and precision ($\pm 0.8\%$ for GC-IRMS), certified standards were analyzed before and after sample runs in the GC-IRMS. All reported $\delta^{13}\text{C}_{\text{FA}}$ values are relative to Vienna Pee Dee Belemnite (VPDB) using the standard notation $\delta^{13}\text{C}_{\text{FA}} (\%) = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$, where R is the corresponding ratio of $^{13}\text{C}/^{12}\text{C}$.

2.4. Data analysis

All data analyses were conducted in R version 4.0.2 (R Core Team 2020). The fatty acid data sets from POM and seals were visualized using correspondence analysis (CA) on non-standardized multivariate data using the *vegan* package (Oksanen et al. 2020). This analysis, with its inherent chi-square distance measure, was selected because of its ability to handle data zeros and compositional data (Greenacre 2011). As these characteristics are inherent in fatty acid data sets, the CA was deemed the most appropriate. Because POM was collected over a broad spatial area, the variance due to station location was removed using a canonical CA (Palmer 1993). Differences between iPOM and pPOM were then tested using a permutation test on the constrained correspondence analysis. A permutational ANOVA between harp and ringed seal fatty acid compositional data was conducted to determine if seal species differed by fatty acid composition. Tests were based on 999 free permutations to test the significance of location and species on the fatty acid profiles of POM and seal groups, respectively.

The 4 specific trophic biomarker fatty acids [16:1(n-7), 20:5(n-3), 18:4(n-3), and 22:6(n-3)] were examined in greater detail, as they were the basis of our trophic biomarker modeling approach. To increase replication and better capture variability in the $\delta^{13}\text{C}_{\text{FA}}$ values from pelagic POM, we included additional data originating from the same region north of Svalbard and the Nansen Basin from a study conducted in 2012 (Kohlbach et al. 2017). A Mann-

Whitney U -test for differences between sample years (2012 and 2017) in the biomarker fatty acid $\delta^{13}\text{C}_{\text{FA}}$ values found no statistical difference (significance was set at $\alpha = 0.05$). We then tested for differences among (1) the mass percentages of the trophic biomarker fatty acids between POM groups and (2) their $\delta^{13}\text{C}_{\text{FA}}$ values between POM groups using the non-parametric Mann-Whitney U -test that is robust for small data sets.

To better visualize differences in all $\delta^{13}\text{C}_{\text{FA}}$ values between harp and ringed seals, we chose a non-metric multidimensional scaling (NMDS) ordination because $\delta^{13}\text{C}_{\text{FA}}$ values are negative. Out of the 34 fatty acids present in seal blubber, 20 common fatty acids that had corresponding $\delta^{13}\text{C}_{\text{FA}}$ values were selected for both seal species. To determine if harp and ringed seals differed by the $\delta^{13}\text{C}_{\text{FA}}$ values, we conducted a permutational ANOVA between groups, based on Euclidean distance (Anderson 2017). Similar to the POM data set, we also investigated the 4 trophic biomarkers in greater detail. We used a Mann-Whitney U -test to test for the differences in their $\delta^{13}\text{C}_{\text{FA}}$ values between harp and ringed seals.

Differences between age classes in both bulk isotopes and fatty acids have been previously reported for harp and ringed seals (Lawson & Hobson 2000, Young et al. 2010). We explored whether this difference was reflected in the $\delta^{13}\text{C}_{\text{FA}}$ values of the trophic biomarkers, in order to determine if age-specific modeling should be conducted. Differences between age classes (young of the year, juveniles, adults) was tested using Kruskal-Wallis rank sum tests as they are appropriate for uneven sample sizes. We found no significant difference between age classes within species groups and therefore pooled all age classes within species.

The proportional contributions of sympagic and pelagic carbon in seal blubber were estimated using the available $\delta^{13}\text{C}_{\text{FA}}$ values of the 4 trophic biomarker fatty acids (mean and standard deviation) of iPOM and pPOM in a Bayesian stable isotope mixing model with the *MixSIAR* package (Stock & Semmens 2016a, Stock et al. 2018). Because we used the $\delta^{13}\text{C}_{\text{FA}}$ values of 4 biomarker fatty acids, and our question focuses on carbon sourcing to blubber, isotopic fractionation was assumed to be zero following similar studies (Budge et al. 2008, Wang et al. 2016). Mixing models were run with 50 000 iterations (where the first 25 000 iterations were discarded). Since the objective of this modeling approach was focused on carbon sourcing, we included a residual error term as recommended by Stock & Semmens (2016b). Modeled estimates of proportional contri-

butions of iPOM and pPOM in seal blubber sum to 1 (100%). This means that seals with minimal sympagic input would have an estimated iPOM contribution near zero. Modeled outputs are reported as the mean contribution of iPOM and pPOM contributions to seal blubber, along with their standard deviation and 95% credibility intervals, i.e. Bayesian confidence intervals.

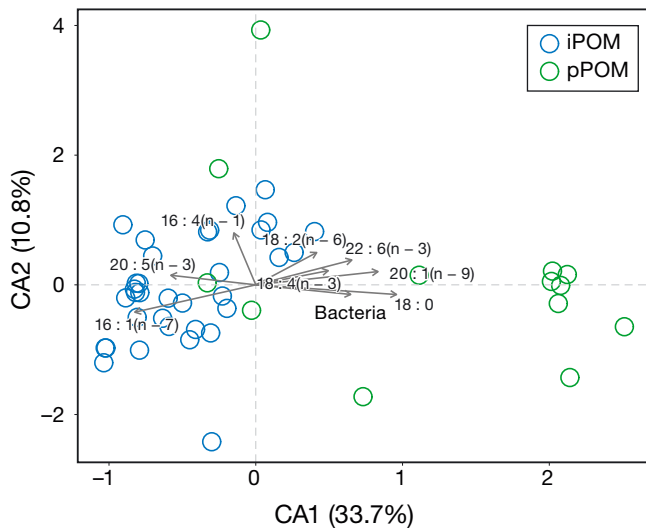


Fig. 2. Correspondence analysis (CA) biplot of 33 compositional fatty acids in particulate organic matter from sea ice (iPOM) and phytoplankton (pPOM). Biplot arrows correspond to significant contribution of fatty acids in the CA ordination. Axis labels indicate percent variance explained for each axis

3. RESULTS

3.1. Particulate organic matter fatty acids and biomarker $\delta^{13}\text{C}_{\text{FA}}$ values

Fatty acid composition between iPOM and pPOM was significantly different ($p = 0.001$) when accounting for the variation due to station locations. The CA axes accounted for 41% of the variability on the fatty acid composition pattern, most likely due to spatial and temporal variability (Fig. 2). Diatom marker fatty acids [16:1(n-7), 20:5(n-3), and 16:4(n-1)] contributed significantly ($p = 0.001$) to the separation of iPOM from pPOM. The dinoflagellate marker fatty acids [18:4(n-3) and 22:6(n-3)] contributed significantly ($p = 0.001$) to pPOM separation, along with 18:0 and bacterial fatty acids (sum of the odd-chain saturated and branched fatty acids across stations) (Fig. 2). Of the 33 fatty acids found in all iPOM samples across stations, 3 dominated in mass contribution: 16:0 (mean $20.9 \pm 4.5\%$), 16:1(n-7) (mean $34.2 \pm 11.1\%$) and 20:5(n-3) (mean $11.0 \pm 5.3\%$) (Fig. 3A, Table S1 in the Supplement at www.int-res.com/articles/suppl/m675p181_supp.pdf). Of the 24 fatty acids found in all pPOM samples across stations, there were again 3 that dominated: 16:0 (mean $25.5 \pm 3.3\%$), 16:1(n-7) (mean $16.5 \pm 12.0\%$), and 18:0 (mean $25.2 \pm 11.0\%$) (Fig. 3A, Table S1).

The mass percentages of the diatom biomarker fatty acids 16:1(n-7) and 20:5(n-3) were significantly different between POM groups ($p \leq 0.0001$, Mann-

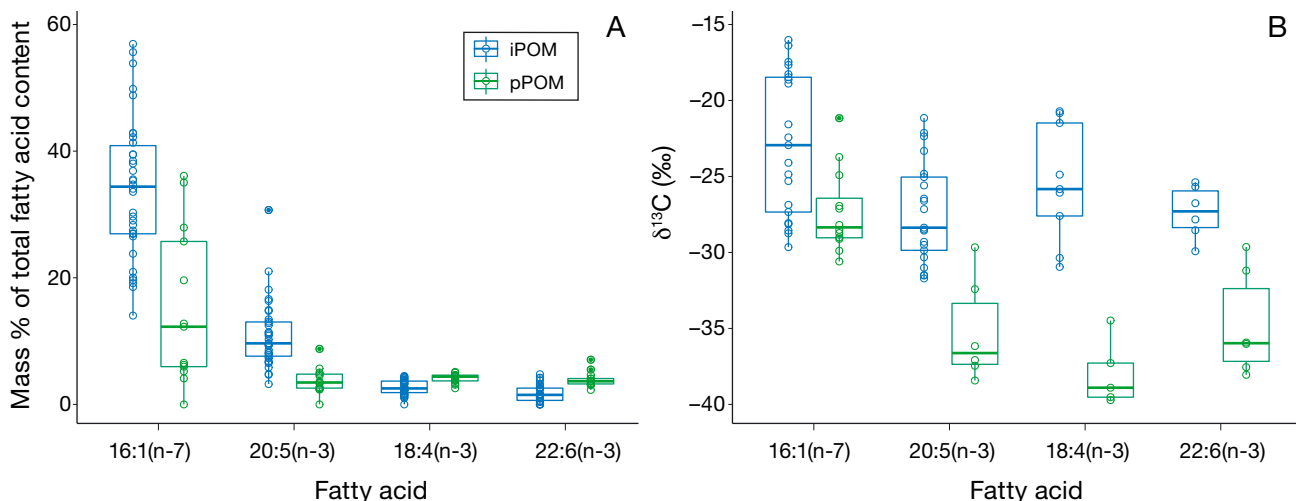


Fig. 3. Relative composition of (A) marker fatty acids and (B) their $\delta^{13}\text{C}_{\text{FA}}$ values compared between POM groups (iPOM: particulate organic matter from sea ice; pPOM: particulate organic matter from phytoplankton). 16:1(n-7) and 20:5(n-3) represent diatom fatty acids; 18:4(n-3) and 22:6(n-3) represent dinoflagellate fatty acids. Horizontal bars within box plots indicate median proportional values; upper and lower portions of the boxes are the approximate 1st and 3rd quartiles. Vertical error bars extend towards the lowest and highest data within a range of 1.5 times the inter-quartile range. Open and closed circles represent data points (closed circles are outliers)

Table 2. Carbon stable isotope means of available $\delta^{13}\text{C}_{\text{FA}}$ values for the 4 biomarker fatty acids included in this study. Mean (± 1 SD) ‰ values of iPOM in 2017 and 2012, pPOM in 2017 and 2012, and of harp seal blubbers sampled in 2016 and ringed seal blubbers sampled in 2017

Fatty acid	iPOM 2017 n = 11 stations	pPOM (2017 & 2012) n = 12 stations	Harp seals 2016 n = 25	Ringed seals 2017 n = 20
16:1(n-7)	-22.87 ± 4.67	-27.32 ± 2.77	-28.26 ± 0.40	-27.11 ± 1.15
20:5(n-3)	-27.37 ± 3.26	-35.20 ± 3.42	-29.55 ± 0.51	-28.54 ± 0.57
18:4(n-3)	-25.41 ± 3.86	-38.45 ± 2.24	-32.99 ± 0.51	-32.62 ± 1.14
22:6(n-3)	-27.35 ± 1.75	-34.73 ± 3.48	-27.93 ± 0.56	-28.16 ± 0.58

Whitney U -test). In comparison, the dinoflagellate biomarker fatty acids were found in relatively smaller amounts in both iPOM [18:4(n-3) mean: $2.8 \pm 1\%$; 22:6(n-3) mean: $2.0 \pm 1.2\%$] and pPOM [18:4(n-3) mean: $4.1 \pm 0.8\%$; 22:6(n-3) mean: $4.0 \pm 0.5\%$]. Regardless of their relative contributions to POM, they were also found to be significantly different ($p < 0.0001$, Mann-Whitney U -test) between POM groups (Fig. 3A).

The $\delta^{13}\text{C}_{\text{FA}}$ values of the 4 marker fatty acids differed significantly ($p \leq 0.005$, Mann-Whitney U -test) between iPOM and pPOM samples, with higher $\delta^{13}\text{C}$ values for iPOM (range: -27.35 to -22.87%) than pPOM (range: -38.45 to -27.32%) for each of the 4 fatty acids (Fig. 3B), enabling their use for the mixing model estimations of carbon sourcing (Table 2).

3.2. Harp and ringed seal fatty acids and $\delta^{13}\text{C}_{\text{FA}}$ values

Based on the relative abundance of all fatty acids found in seal blubber (Table S1), there was significant ($p = 0.001$) group separation between species. The CA axes accounted for 70% of the variability in the fatty acid composition pattern (Fig. 4A). Within the first ordination axis of all fatty acids, the diatom biomarkers 16:1(n-7) and 20:5(n-3), and the dinoflagellate marker 18:4(n-3), were more prevalent in the harp seal samples, while the dinoflagellate biomarker 22:6(n-3) was more prevalent in the ringed seal samples (Fig. 4A). The separation of seal blubber composition along the first axis was primarily driven by the monounsaturated fatty acids (MUFAs) with 16, 18, and 20 carbon atoms. Both seal species had assimilated 20:1 and 22:1 MUFAs, including their specific isomers, with slightly higher levels in ringed seals. The *Calanus* spp. biomarker fatty acids [sum of 20:1(n-9) and 22:1(n-11)] contributed more to the ringed seals than to the harp seals. Despite group separation, the same fatty acids contributed the high-

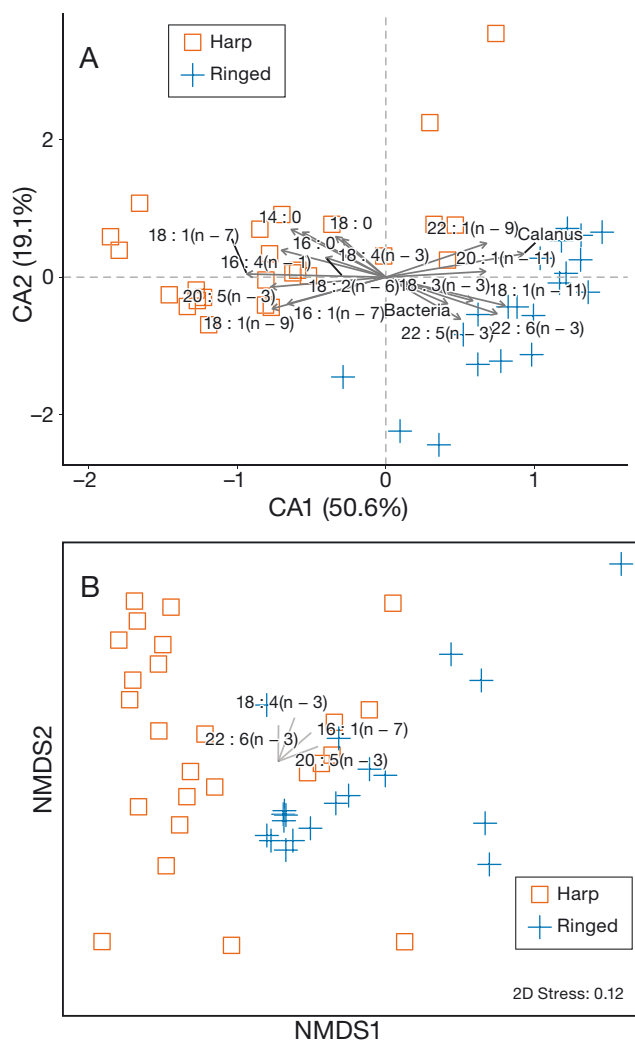


Fig. 4. Harp and ringed seal patterns of fatty acids and their carbon isotope values. (A) Correspondence analysis (CA) biplot of 34 compositional fatty acids in harp and ringed seals. Biplot arrows correspond to significant contributions from fatty acids in the CA ordination. Axis labels indicate percent variance explained for each axis. (B) Nonmetric multidimensional scaling of the $\delta^{13}\text{C}_{\text{FA}}$ values for 20 fatty acids in the blubber of harp and ringed seals. Biplot lines depict directions of marker fatty acids

est mean (\pm SD) mass percentages for both seal species: 14:0 ($5.2 \pm 0.5\%$ in harp seals, $3.3 \pm 0.3\%$ in ringed seals), 16:0 ($9.3 \pm 1.4\%$ in harp, $7.0 \pm 1.4\%$ in ringed), the 18:1 MUFA family ($26.8 \pm 1.2\%$ in harp, $24.9 \pm 1.2\%$ in ringed), and 20:1(n-9) ($7.7 \pm 2.3\%$ in harp, $12.3 \pm 2\%$ in ringed) (Table S1).

The NMDS ordination for $\delta^{13}\text{C}_{\text{FA}}$ values in harp and ringed seal blubber showed significant separation between the 2 seal species ($p = 0.001$), though with more overlap than the fatty acid data (Fig. 4B). The separation was prominent along NMDS axis 1 and associated with 20:5n-3 and 16:1n-7, with no separation along NMDS axis 2. The $\delta^{13}\text{C}_{\text{FA}}$ values of many fatty acids fell in a similar range for both harp and ringed seals (Fig. S1 in the Supplement). For the 4 biomarker fatty acids, ringed seals had significantly higher $\delta^{13}\text{C}_{\text{FA}}$ values for 16:1(n-7) and 20:5(n-3) than harp seals, while there were no significant differences between the $\delta^{13}\text{C}_{\text{FA}}$ values for 18:4(n-3) and 22:6(n-3) between the seal species (Table 2, Fig. 5).

3.3. iPOM and pPOM contributions to seal blubber — from mixing models

Mixing models using the 4 trophic biomarker fatty acids estimated the proportional contribution (1 = 100 %) of iPOM and pPOM $\delta^{13}\text{C}_{\text{FA}}$ in seal blubber. Mixing models including both seal species estimated

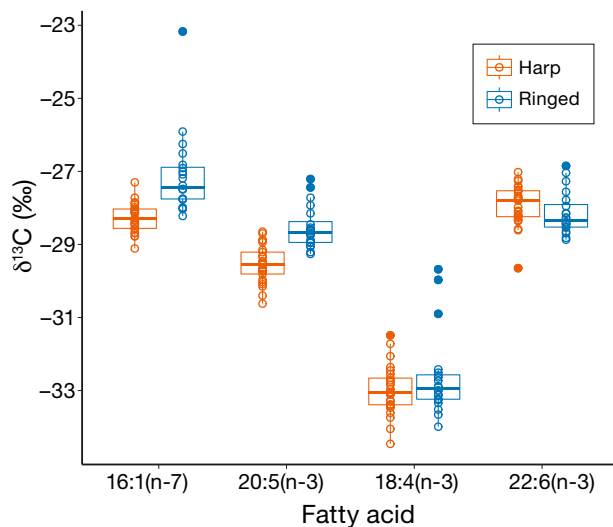


Fig. 5. Trophic biomarker $\delta^{13}\text{C}_{\text{FA}}$ values compared between seal species. Horizontal bars within box plots indicate median proportional values; upper and lower portions of the boxes are the approximate 1st and 3rd quartiles. Vertical error bars extend towards the lowest and highest data within a range of 1.5 times the inter-quartile range. Open and closed circles represent data points (closed circles are outliers)

Table 3. Estimates of iPOM and pPOM contributions (mean \pm 1 SD with 95 % Bayesian credible intervals) to harp (2016) and ringed (2017) seals from stable isotope mixing models using the 4 marker fatty acids (shown in Table 2)

	N	Mean \pm SD	Lower 95 % credible interval	Higher 95 % credible interval
Harp seal				
iPOM	25	0.69 ± 0.08	0.54	0.85
pPOM		0.31 ± 0.08	0.15	0.46
Ringed seal				
iPOM	20	0.72 ± 0.07	0.59	0.86
pPOM		0.28 ± 0.07	0.14	0.41

the group mean iPOM contributions to harp seals to be 0.69 ± 0.08 and pPOM to be 0.31 ± 0.08 . For ringed seals, mean iPOM contributions were 0.72 ± 0.07 and pPOM contributions were 0.28 ± 0.07 (Table 3).

4. DISCUSSION

4.1. Fatty acids in iPOM and pPOM

The overall fatty acid composition in our iPOM samples was similar to that in other Arctic studies (Falk-Petersen et al. 1998, Budge et al. 2008, Kohlbach et al. 2016). The diatom marker 16:1(n-7) contributed the highest mass percentage in our iPOM samples, and the ratio of 16:1(n-7)/16:0 was >1 in our iPOM samples also suggesting a dominance of diatoms (Graeve et al. 1994). The second diatom marker 20:5(n-3) also had considerably higher proportions in iPOM compared to pPOM (Leu et al. 2006). Interestingly, in the Bering Sea, Wang et al. (2014) found that 20:5(n-3) contributed more than 16:1(n-7), the opposite of our findings, which could be related to differing diatom community composition or differing bloom growth conditions and phenology. Budge et al. (2008) suggested that the combination of high contributions of 16:1(n-7) and low levels of polyunsaturated fatty acids (PUFAs) (in their case, 18.5 %) might be an indication of rapid algal growth conditions. The average contribution of 16:1(n-7) in the present study was 34 %, with moderate levels of total PUFAs (22.8 %), which is not clearly indicative of rapid growth conditions. Based on metabarcoding from the sea-ice cores sampled at our ice stations in 2017, dinoflagellates were present (B. Hassett pers. comm.). This is consistent with earlier findings (Booth & Horner 1997) and supported by the presence of 18:4(n-3) and 22:6(n-3) in our iPOM samples. Dinoflagellates and the hapto-

phyte *Phaeocystis pouchetti* can be common in several Arctic ice habitats, including the snow–ice interface of first-year ice, in refrozen leads, and in melting ice (Tamelander et al. 2009, Assmy et al. 2017, Fernández-Méndez et al. 2018), and our late ice stations occurred during advanced stages of melt.

The major contributing fatty acids found in our pPOM samples were also similar to data from other Arctic food web studies (Falk-Petersen et al. 1998, Wang et al. 2014, Kohlbach et al. 2016). During a seasonal study in a High Arctic fjord (Kongsfjorden, Svalbard) near our study area, the flagellate markers 18:4(n-3) and 22:6(n-3) had even higher contributions in pPOM when compared to our values (Mayzaud et al. 2013). These findings suggest differences in nutrient availability or species composition between these areas. In addition to the protist taxa discussed, the occurrence of bacteria (the odd-chain saturated and branched fatty acids) in both iPOM and pPOM demonstrates that POM constitutes a complex mix of microbial species (Kirst & Wiencke 1995) with strong potential for seasonal and regional changes driven by bloom phenology.

4.2. $\delta^{13}\text{C}$ differences in biomarker fatty acids between habitats

The differences we found in the $\delta^{13}\text{C}_{\text{FA}}$ marker values between iPOM and pPOM is the key prerequisite to using these trophic markers in the subsequent mixing models. This finding is in agreement with an earlier study from the Nansen Basin when both first-year and multi-year ice were studied (Kohlbach et al. 2016: $\delta^{13}\text{C}_{\text{FA}}$ iPOM: -28.4 to -23.4‰ ; $\delta^{13}\text{C}_{\text{FA}}$ pPOM: -39.3 to -26.4‰) and with a study of seasonal first-year ice in the Bering Sea (Wang et al. 2014: $\delta^{13}\text{C}_{\text{FA}}$ iPOM: -26.5 to -21.0‰ ; $\delta^{13}\text{C}_{\text{FA}}$ pPOM: -30.4 to -27.0‰). Leu et al. (2020) found an increasing trend in $\delta^{13}\text{C}_{\text{FA}}$ values in a seasonally sea-ice-covered fjord in Svalbard throughout spring (April–May), suggesting that bloom succession and an increase in under-ice light play a role in these values, similar to seasonal changes determined by bulk $\delta^{13}\text{C}$ values. To date, studies investigating $\delta^{13}\text{C}_{\text{FA}}$ values of individual fatty acids in POM throughout the Arctic are not as ubiquitous compared to studies of bulk $\delta^{13}\text{C}$ POM. Isotopic enrichment in bulk $\delta^{13}\text{C}$ values in iPOM over pPOM is seasonally and regionally variable, depending on environmental and physiological factors in addition to taxonomic community composition and biomass, which can be minimal or absent at times (de la Vega et al. 2019, Leu et al. 2020).

4.3. Fatty acid composition of harp and ringed seals

Although we cannot determine exactly where the harp seals from this study were foraging, it is likely they were following the sea-ice-edge in the weeks or months before collection (Stenson et al. 2020). The presence of the *Calanus* spp. trophic biomarkers in their blubber suggest that they were feeding on a *Calanus* spp.-derived food chain (Sargent & Falk-Petersen 1988). This food chain supports a variety of their major prey items. During late summer and early autumn in the northern Barents Sea, harp seals feed on pelagic crustaceans such as krill (*Thysanoessa* spp.), hyperiid amphipods *Themisto libellula*, and polar cod (Lydersen et al. 1991, Nilssen et al. 1995b, Falk-Petersen et al. 2004). These species, also supported by the *Calanus* spp. food chain, can have high levels of 16:1(n-7) and 20:5(n-3) (Auel et al. 2002, Falk-Petersen et al. 2000, Kohlbach et al. 2017).

The diet of ringed seals is often dominated by polar cod (e.g. Labansen et al. 2007), but they also consume a mix of other fishes and crustaceans (Gjertz & Lydersen 1986, Weslawski et al. 1994). Along the west coast of Svalbard, ringed seal diet (determined from the same fjord as the animals in the present study) has recently been shown to be dominated by polar cod (Bengtsson et al. 2020). 16:1(n-7) and 20:5(n-3), while slightly lower in ringed seals than in harp seals, were still major contributing fatty acids, similar to that found in previous studies (Thiemann et al. 2007, Cooper et al. 2009). Regardless of season, ringed seals from the Bering and Chukchi Seas (Wang et al. 2016) had higher contributions of 16:1(n-7), 20:5(n-3), and 22:6(n-3), and lower contributions of 18:4(n-3) than the ringed seals from this study, potentially resulting from differences in the biomarker-producing algal communities as indicated in the observed differences in the iPOM and pPOM fatty acids (Wang et al. 2014).

4.4. Carbon sourcing to seal diets

Based on the 4 specific trophic biomarkers, we found that part of the species separation is due to significantly higher $\delta^{13}\text{C}_{\text{FA}}$ values of 16:1(n-7) and 20:5(n-3) in ringed seals compared to harp seals. This finding indicates that ringed seals assimilated more sympagic fatty acids compared to harp seals. Our ringed seals had similar $\delta^{13}\text{C}_{\text{FA}}$ values of the diatom marker 20:5(n-3) (-28.5‰) to Bering Sea ringed seals (-29.2‰ ; Wang et al. 2016), yet were more negative when compared to ringed seals from land-fast ice in

Utqiagvik, Alaska (-26.4‰) (Budge et al. 2008). For the $\delta^{13}\text{C}_{\text{FA}}$ values for 18:4(n-3) and 22:6(n-3), the ringed seals in this study had higher values compared to the ringed seals in the Bering Sea (Wang et al. 2016). No comparable values are currently available for harp seals.

Our modeling results showed that both harp and ringed seal diets are strongly supported by sea-ice-derived carbon sources. It should be noted that in addition to different carbon sources, other factors might be contributing to these differences (see section 4.5). Regardless of year or region, earlier studies also found that harp seal diet is supported by sea-ice production and a diatom-based food web (Falk-Petersen et al. 2004, 2009). In late summer and early autumn, harp seals maintain strong affinities to the marginal ice zone (Folkow et al. 2004, Nordøy et al. 2008), due to the seasonally strong pulses of marine productivity in this area (Falk-Petersen et al. 1990, Wassmann et al. 2020). Modeled results of sea-ice-derived carbon contributions to various harp seal prey items found that iPOM contributed up to 55% in the amphipod *T. libellula* (Kohlbach et al. 2016), and up to 65% in polar cod (Kohlbach et al. 2017). If we follow the sea-ice carbon pathway from the prey of the seals, it is plausible that at the time of the year the harp seals in this study were collected (before their long southward migration), sympagic carbon sources contributed more to their diet than pelagic carbon.

For ringed seals, the maximum value estimates of sea-ice-derived carbon contributions were similarly high when compared to other modeled values. In the Pacific Arctic, sea-ice-derived carbon in ringed seal blubber ranged from 24 to 60% in the Bering Sea, depending on time of year (Wang et al. 2016), and up to 62% in land-fast ice off the coast of Utqiagvik, Alaska (Budge et al. 2008). Despite minor methodological differences between the studies, there is strong overall agreement on the high contributions of ice-derived carbon to ringed seal diets. Land-fast ice is seasonally present where the ringed seals from this study were captured (Nilsen et al. 2008), which could have potentially supported the high sympagic contributions found in their blubber. In turn, land-fast ice can contain substantial amounts of ice algae that become available for the marine food web (Thyrring et al. 2017). Similar to harp seals, ringed seals replenish energy stores that were used during the spring (Ryg et al. 1990, Young & Ferguson 2013). An alternative to land-fast ice-derived carbon sources, late summer/early autumn foraging trips to the ice edge (Freitas et al. 2008, Lone et al. 2019) could also explain the high iPOM contributions in their blubber.

Based on the methods applied in our study, we conclude that both species of ice seals had substantial contributions of sea-ice-derived organic carbon in their diets (which were reflected in their blubber). These data are consistent with observations from other Arctic areas for both ice seals and their prey.

4.5. Model sensitivity and caveats

Modeling carbon contributions from sea ice and phytoplankton to blubber in near-apex predators warrants a discussion of both model sensitivities and caveats.

4.5.1. Issue 1

The fatty acid biomarkers used for this study were selected because they remain unmodified as they move through the marine food web (Dalsgaard et al. 2003). Almost all PUFAs originate from primary producers but can undergo trophic modifications as they pass upwards in a food chain (Bell & Tocher 2009). Vertebrates are unable to synthesize PUFAs de novo, and these essential fatty acids must be acquired through their diet (Tinoco 1982). However, vertebrates possess metabolic pathways to further desaturate and elongate the n-3 PUFAs (Rosenthal 1987) to form other highly unsaturated fatty acids (Bell & Tocher 2009). It has been shown that some pinniped species can modify various dietary fatty acids differently while consuming the same prey type, demonstrating the variability of assimilation within consumers (Rosen & Tollit 2012). Therefore, we combined fatty acids with their $\delta^{13}\text{C}_{\text{FA}}$ values in our study, in order to provide a finer resolution of the trophic biomarkers of interest.

4.5.2. Issue 2

It is well known that Bayesian model results can be skewed when not accounting for trophic fractionation (i.e. the amount of variation in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between prey and predators) in bulk carbon and nitrogen isotopes in diet reconstruction studies (Bond & Diamond 2011). Our study avoided this potential pitfall because we worked with compound-specific stable isotope values of carbon of individual trophic marker fatty acids. However, we assume here that fatty acids are integrated into seal blubber with little to no modification of their carbon chain, thus displaying unchanged $\delta^{13}\text{C}_{\text{FA}}$ values (Issue 1). Iso-

topic fractionation, particularly for 2 of the primary producer fatty acids used in this study, was found to be negligible for Arctic eider ducks (*Polysticta stelleri* and *Somateria fischeri*) and Atlantic pollock *Pollachius virens* (Budge et al. 2011, 2016). Experimental work on these vertebrate species found no trophic discrimination of the 20:5(n-3) and 22:6(n-3) $\delta^{13}\text{C}_{\text{FA}}$ values in either adipose tissue or serum, suggesting unmodified uptake of these fatty acids (Budge et al. 2011, 2016). These findings would then justify subsequent studies using no fractionation factor when quantifying carbon contributions to diet using trophic marker fatty acids (Kohlbach et al. 2016, 2017, Wang et al. 2016). The modeled results of sea-ice carbon to seal prey in this region (see section 4.4) would hence further support the relatively high contributions we found in the modeled results for seals. Using the $\delta^{13}\text{C}_{\text{FA}}$ values of only 20:5(n-3) and 22:6(n-3) in our mixing model (rather than all four), for comparability with Wang et al. (2016), the estimated contributions of sympagic carbon in seal blubber were even higher for both species in the present study ($\geq 79\%$). These differences show that the mixing model approach is also sensitive to which fatty acids are chosen as biomarkers for diatoms and dinoflagellates.

Including isotopic fractionation terms into the model would certainly be more accurate, but to our knowledge only few data are available for higher marine organisms (see above). Furthermore, experimental work has shown that $\delta^{13}\text{C}_{\text{FA}}$ values of PUFAs can also be modified via fractionation when being incorporated into lipids in various tissues (Gladyshev et al. 2016), or by metabolic processes (Chiappella et al. 2021). Although it is difficult to map the individual steps of isotopic fractionation into total metabolism, we recognize a need for increased attention towards the kinetics of metabolic processes. This will better our understanding of the processes that cause fractionation, resulting in better application of $\delta^{13}\text{C}_{\text{FA}}$ values in quantitative models. Nonetheless, our results can be over- or under-estimations due to shifting trophic baselines in aquatic ecosystems (de la Vega et al. 2019, Casey & Post 2011) and the complexities of isotopic discrimination in marine mammals (Newsome et al. 2010).

4.5.3. Issue 3

We found high contributions of iPOM in the seals' diets. This result is, at first sight, surprising given that the contribution of sea-ice production is generally lower than pelagic primary production and the pro-

ductive season in ice is short and regionally variable in seasonal ice-covered regions. Sympagic production in the Barents Sea along the spring ice edge ranges between 4.9 and 55 mg (0.0049–0.055 g) $\text{C m}^{-2} \text{d}^{-1}$ (McMinn & Hegseth 2007), which is at least one order of magnitude below pelagic gross primary production in this region, which is estimated at 0.19 to 0.85 g $\text{C m}^{-2} \text{d}^{-1}$ (Svensen et al. 2019). Ice algal production in the Northern Barents Sea is estimated to be approximately 5.3 g $\text{C m}^{-2} \text{yr}^{-1}$ (Hegseth 1998), while the deep Arctic basins can have daily rates as high as 0.013 to 0.069 g $\text{C m}^{-2} \text{d}^{-1}$ (Gosselin et al. 1997, Fernández-Méndez et al. 2015). Again, this annual estimate is well below the phytoplankton production on the nutrient-rich inflow shelves such as the Barents Sea (over 70 g $\text{C m}^{-2} \text{yr}^{-1}$) but in the same range as phytoplankton production in the central Arctic Ocean (Wiedmann et al. 2020). It should be noted that the highest phytoplankton production contributions occur in ice-free areas and, as such, might not be an important carbon source for the ice-based seals. Consequently, if seal foraging occurred over large parts off the shelves in deep ice-covered Arctic waters or if they spent a considerable amount of time close to sea ice, relatively high contributions of ice algal carbon could be expected.

4.5.4. Issue 4

Assumptions were made with spatial and temporal variability of POM, and sampling did not always occur within optimal time frames. We sampled POM from a large geographic area, in order to capture more of the variation of the $\delta^{13}\text{C}_{\text{FA}}$ values. We believe this was an appropriate approach, given that these seals are highly mobile predators within the European Arctic.

Pelagic $\delta^{13}\text{C}_{\text{FA}}$ values were included from a different year, which is suboptimal because sea-ice- and pelagic-derived carbon sources likely vary in their contribution to consumers temporally (as well as spatially). While the temporal mismatch between sampling of carbon end members and seal sampling is not ideal, we argue that the variation in pPOM carbon isotope values has been shown to be rather minor between years and seasons in the study area region (Søreide et al. 2006: bulk $\delta^{13}\text{C}$: -24.6 to -21% ; Tamelander et al. 2006: bulk $\delta^{13}\text{C}$: -26.5 to -23.0%). When comparing $\delta^{13}\text{C}_{\text{FA}}$ values, our pPOM values are similar to published results from the Nansen Basin (see section 4.2). iPOM values, however, are both regionally and seasonally variable in this and

other study areas, but interannual variation is not higher than seasonal and regional variation of iPOM (Søreide et al. 2006, Tamelander et al. 2006).

We did not always sample seal tissues in the optimal time frame relative to source turnover. The slight off-set of end-member sampling and seal sampling is preferred because of the turnover time needed to assimilate dietary fatty acids in seal blubber (Tollit et al. 2010). Fatty acids found in blubber reflect a time period of weeks to several months for seals (Nordstrom et al. 2008, Tollit et al. 2010). We hence evaluate the mismatch of end-member sampling and seal sampling as comparatively minor for pPOM, though iPOM estimates could be more heavily affected. Given that our estimates of iPOM contributions are very high, even a somewhat lower estimate would not change the conclusion substantially, since estimates of 40–60% iPOM contribution would still be considered high and confirm the conclusion of a strong and rather similar ice association for both species. Seasonal or monthly variation in the contribution of iPOM can be expected (Wang et al. 2016) but was not resolved in our study.

5. CONCLUSIONS

In summary, we found differences in both fatty acids and the $\delta^{13}\text{C}_{\text{FA}}$ values of specific trophic biomarkers in sympagic algae and phytoplankton as hypothesized. In contrast to our expectations, the 2 seal species were strongly separated in all fatty acid patterns, indicating a significant degree of dietary niche separation. Even though we found no differences in age classes for the 4 trophic biomarkers, our sample sizes were relatively small and disproportionate within age classes; hence, we recommend a complementary study where age-class differences could be more thoroughly explored. Finally, we hypothesized that sympagic carbon would be more likely to contribute to the diet of ringed seals because of their stronger association with sea ice. Instead, we found that sympagic carbon supported both harp and ringed seals similarly over the summer and into autumn (June, August, and September).

Since 2011, the Eurasian Basin has been almost ice free at the end of summer, with <10% sea-ice coverage remaining, and this area has experienced a continual northward retreat of sea-ice extent (Polyakov et al. 2017). Concomitantly, occurrences of new Atlantic fish species have been found in ringed seal diet (Bengtsson et al. 2020), as these boreal species expand into the Arctic (Renaud et al. 2012). Regard-

less of these changes, sea ice is still seasonally present within the European Arctic, and both harp and ringed seals continue to associate with this habitat. Their continued association with sea ice is reflected in their foraging behavior (Hamilton et al. 2016, 2021) and migratory patterns (Stenson et al. 2020), and is still apparent in the carbon sourcing to their diet (the present study). Given the current state of sea-ice loss in the Northern Barents Sea (Perovich et al. 2020), it remains to be seen if these seals will transition to a more open-water dominated lifestyle and diet, opt for potentially longer migration routes to the ice edge, or experience population size declines.

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