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Carbon sources and trophic relationships of ice seals during recent environmental shifts in the Bering Sea

Shiway W. Wang,[1,2,5] Alan M. Springer,[1] Suzanne M. Budge,[3] Lara Horstmann,[1] Lori T. Quakenbush,[4] and Matthew J. Wooller[1,2]

[1]*Institute of Marine Science, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, Alaska 99775 USA*
[2]*Alaska Stable Isotope Facility, Water and Environmental Research Center, Institute of Northern Engineering, University of Alaska Fairbanks, Fairbanks, Alaska 99775 USA*
[3]*Department of Process Engineering and Applied Science, Dalhousie University, Halifax, Nova Scotia B3H 4R2 Canada*
[4]*Alaska Department of Fish and Game, Fairbanks, Alaska 99701 USA*

Abstract. Dramatic multiyear fluctuations in water temperature and seasonal sea ice extent and duration across the Bering–Chukchi continental shelf have occurred in this century, raising a pressing ecological question: Do such environmental changes alter marine production processes linking primary producers to upper trophic-level predators? We examined this question by comparing the blubber fatty acid (FA) composition and stable carbon isotope ratios of individual FA ($\delta^{13}C_{FA}$) of adult ringed seals (*Pusa hispida*), bearded seals (*Erignathus barbatus*), spotted seals (*Phoca largha*), and ribbon seals (*Histriophoca fasciata*), collectively known as "ice seals," sampled during an anomalously warm, low sea ice period in 2002–2005 in the Bering Sea and a subsequent cold, high sea ice period in 2007–2010. $\delta^{13}C_{FA}$ values, used to estimate the contribution to seals of carbon derived from sea ice algae (sympagic production) relative to that derived from water column phytoplankton (pelagic production), indicated that during the cold period, sympagic production accounted for 62–80% of the FA in the blubber of bearded seals, 51–62% in spotted seals, and 21–60% in ringed seals. Moreover, the $\delta^{13}C_{FA}$ values of bearded seals indicated a greater incorporation of sympagic FAs during the cold period than the warm period. This result provides the first empirical evidence of an ecosystem-scale effect of a putative change in sympagic production in the Western Arctic. The FA composition of ice seals showed clear evidence of resource partitioning among ringed, bearded, and spotted seals, and little niche separation between spotted and ribbon seals, which is consistent with previous studies. Despite interannual variability, the FA composition of ringed and bearded seals showed little evidence of differences in diet between the warm and cold periods. The findings that sympagic production contributes significantly to food webs supporting ice seals, and that the contribution apparently is less in warm years with low sea ice, raise an important concern: Will the projected warming and continuing loss of seasonal sea ice in the Arctic, and the associated decline of organic matter input from sympagic production, be compensated for by pelagic production to satisfy both pelagic and benthic carbon and energy needs?

Key words: bearded seal; climate change; compound-specific stable isotope analysis; fatty acids; food web ecology; ice algae; phytoplankton; ribbon seal; ringed seal; sea ice loss; spotted seal.

Introduction

The Arctic has warmed at nearly twice the rate of the rest of the world in recent decades, and the trend is expected to continue through this century, with a nearly sea ice-free Arctic in September projected by 2037 (ACIA 2004, Wang and Overland 2009, 2012). Arctic sea ice extent has decreased in virtually all regions since the beginning of the satellite record in 1979, with the exception of the Bering Sea during winter (Perovich et al. 2013). In the Bering Sea, the extent of winter sea ice varies between years, but over the past several decades it has shown a gradually increasing trend (Wendler et al. 2014). Nevertheless, dramatic multiyear fluctuations in temperature and sea ice extent have occurred in this century, characterized by anomalously warm air and water temperatures and low winter and spring sea ice extent in 2001–2005 that shifted abruptly to cold years with markedly colder air and water temperatures and greater ice since 2007 (Stabeno et al. 2007, 2012, NSIDC 2011). For example, the average amount of total ice cover in March and April at a long-term biophysical mooring on the eastern Bering Sea shelf (site M2; 163°–165° W, 56.5°–57.5° N) was less than 5% between 2000 and 2005, but increased to 53% in 2007 and almost 65% in 2010 (Stabeno et al. 2012). Years with minimal ice cover in

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[5]E-mail: shiway@gmail.com

March and April had daily depth-averaged water temperatures up to 3°C higher than average, while years with heavy sea ice had average temperatures as much as 3°C lower than average (Stabeno et al. 2012).

The extent of winter sea ice and the timing of the spring ice retreat in the Arctic affect the timing and magnitude of spring phytoplankton blooms, which can be seeded by sea ice algae (e.g., Niebauer et al. 1990, Spindler 1994, Bluhm and Gradinger 2008). Since at least 1999, the length of the open water season in the Bering Sea has been correlated positively with annual new primary production (NPP) by pelagic phytoplankton (Brown and Arrigo 2012). Thus, annual NPP in the warm, early 2000s tended to be higher than in colder years before or since. Similar estimates of production by sea ice algae (sympagic production) have not been made, although it would be expected that sympagic production was lower in the warm, light sea ice period than in the subsequent cold, heavy ice period. Such documented and potential changes in the timing and quantity of primary production by these two sources could alter food web dynamics in the Arctic (Grebmeier et al. 2006, Bluhm and Gradinger 2008, Grebmeier 2012) by affecting lower trophic level consumers like zooplankton (e.g., Leu et al. 2011) and benthic invertebrates (e.g., Sun et al. 2009), and thus species at higher trophic levels in both pelagic and benthic food webs.

Ice seals, which include ringed seals (*Pusa hispida*), bearded seals (*Erignathus barbatus*), spotted seals (*Phoca largha*), and ribbon seals (*Histriophoca fasciata*), so named because of their strong associations with sea ice habitat, are prominent among the higher trophic level predators that might be affected by changes in sea ice and its role in food web production. All four species depend upon sea ice as a substrate on which to rest in winter and give birth in spring, although particular habitat preferences differ among species within the sea ice environment (e.g., Simpkins et al. 2003). Diets of all ice seals include pelagic and benthic fishes and invertebrates in amounts that vary spatially and temporally and among species (e.g., McLaren 1958, Burns 1971, Lowry et al. 1980*a,b*, Antonelis et al. 1994, Dehn et al. 2007). In part because of potential changes in diet due to sea ice loss, and consequences to individual and population health, the Arctic Basin population of ringed seals and the Pacific population of bearded seals were listed as threatened under provisions of the U.S. Endangered Species Act in 2012 (NMFS 2012*a,b*).

Our broad goal in this study was to gain insight into production and food web dynamics in the Bering Sea in relation to environmental conditions, and thus be better able to anticipate long-term effects of climate change on this highly productive marine ecosystem. If the ratio of pelagic:sympagic primary production declined between the recent warm and cold periods, pelagic and benthic community structure and predator–prey relationships also might have been altered, and a signal of that change might have been recorded in species at high trophic levels, such as ice seals. We examined this possibility by using the fatty acid (FA) composition of ice seal blubber and stable carbon isotope composition of individual FAs ($\delta^{13}C_{FA}$) to (1) determine if diets changed seasonally within species (spring–summer vs. fall–winter months), (2) examine geographic and interannual variability in diets within species, (3) estimate the proportional contribution of pelagic and sympagic carbon sources to seal diets during the recent cold period, and (4) assess the importance of these two carbon sources in the recent warm and cold periods in the Bering Sea. FA analysis has been used widely to study diets of marine mammals (e.g., Iverson et al. 1997, Thiemann et al. 2007, Cooper et al. 2009), and by combining stable isotope analysis with FA analysis, more detailed information on pathways of carbon and energy transfer through food webs can be obtained (Budge et al. 2008, Graham et al. 2014, Wang et al. 2015).

Methods

Sample collection

Full-depth blubber samples (skin to muscle), taken from the trunk of the bodies of ice seals, were obtained opportunistically from Alaskan Native subsistence hunters in the communities of Hooper Bay, Gambell, Savoonga, Nome, and Little Diomede in the Bering Sea, and Shishmaref, Kivalina, and Point Hope in the Chukchi Sea (Fig. 1). The exact location on the trunk where blubber samples were taken was not known, but we assumed this did not affect the analyses because blubber FA composition of pinnipeds is uniform across the body (Koopman et al. 1996, Cooper 2004, Lambert et al. 2013). Samples were collected as soon as possible after death and frozen at −20°C until they arrived at the laboratory. Subsamples were taken using a clean scalpel and a glass cutting board; any oxidized tissue was removed and the sample was wrapped tightly in aluminum foil and frozen at −80°C in air-tight bags until analysis. Ringed seal samples were collected in 2003–2010, bearded seal samples were collected in 2002–2010, spotted seal samples were collected in 2003–2009, and ribbon seal samples were collected in 2003 and 2008 (Table 1; Appendix S1). The adult bearded seal FA data from 2002 were from Budge et al. (2007), and FA data for 31 adult ice seals from 2003 were from Cooper et al. (2009). Sample sizes by season, year, and location are given in Appendix S1. The actual timing of harvest, sample collection, and sample size was dependent on ice and weather conditions and seal availability. Ages of seals were estimated by counting cementum growth layers of sectioned teeth (Matson's Laboratory, Manhattan, Montana, USA), with one growth layer group representing 1 yr of age (Mansfield and Fisher 1960, Benjaminsen 1973, Stewart et al. 1996). All samples were collected as part of an ongoing biomonitoring program by the Alaska Department of Fish and Game under National Marine Fisheries Service Scientific Research Permit No. 358-1787.

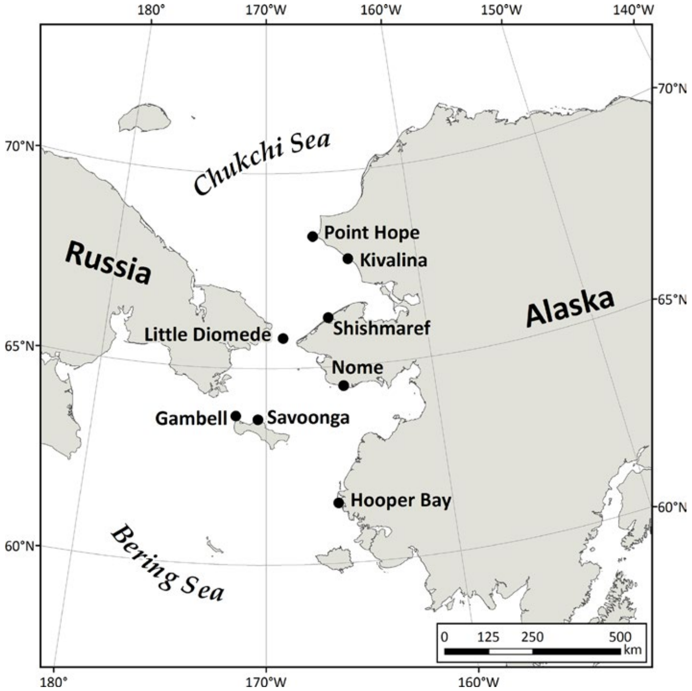

FIG. 1. Map showing the locations of Alaska Native subsistence communities, where blubber samples of adult ringed, bearded, spotted, and ribbon seals were collected. Image by J. Crawford.

TABLE 1. Samples sizes for blubber collected from adult ringed, bearded, spotted, and ribbon seals by year and season.

Year	Season	Ringed seal	Bearded seal	Spotted seal	Ribbon seal
2002	spring–summer	0	7	0	0
	fall–winter	0	0	0	0
2003	spring–summer	1	6	9 (2)	15 (5)
	fall–winter	5	0	1	0
2004	spring–summer	1	7	1	0
	fall–winter	0	2	2	0
2005	spring–summer	2	25 (23)	0	0
	fall–winter	3	0	3	0
2006	spring–summer	1	6 (5)	2	0
	fall–winter	3 (2)	0	1	0
2007	spring–summer	2	8	0	0
	fall–winter	3	0	7	0
2008	spring–summer	2	11 (10)	0	1
	fall–winter	10	0	14	0
2009	spring–summer	7	10	0	0
	fall–winter	8	0	11	0
2010	spring–summer	3	20	0	0
	fall–winter	0	0	0	0
Total		51 (50)	102 (98)	51 (44)	16 (6)

Notes: All samples were analyzed for fatty acids. Numbers in parentheses are the sample sizes available for the $\delta^{13}C_{FA}$ analysis, if different from the number analyzed for fatty acids.

Laboratory analysis

Blubber FAs reflect an average of prey acquired over weeks to several months (Iverson et al. 2004, Nordstrom et al. 2008, Tollit et al. 2010). Previous studies of FAs in pinniped blubber have found that the inner half reflects a more recent diet, while the full-depth layer provides information on the longer-term diet (reviewed in Tollit et al. 2010). Since the shortest dietary time frame that we were interested in was over a period of 6 months (see

Data analysis), we analyzed the full-depth blubber sample, which would likely give the most information about the diet incorporated over that time. Thus, a longitudinal slice (approximately 500 mg) of full-depth blubber was sub-sampled, and any skin and muscle were removed. Lipids were extracted from all samples using 2:1 chloroform/methanol (Folch et al. 1957, Parrish 1999). Fatty acid methyl esters (FAME) were prepared using an acidic transesterification procedure (Budge et al. 2006). FAME were quantified using temperature-programmed gas chromatography (GC) on a Perkin Elmer Autosystem II Capillary FID gas chromatograph (Perkin Elmer, Boston, MA, USA) fitted with a 30 m × 0.25 mm internal diameter column coated with 50% cyanopropyl-methylpolysiloxane (DB-23) and linked to a computerized integration system (Varian Star software, Agilent Technologies, Santa Clara, CA, USA) at Dalhousie University according to Budge et al. (2006). Shorthand nomenclature of A:Bn-X was used to describe each FAME, where A represents the number of carbon atoms, B the number of double bonds, and X the position of the double bond closest to the terminal methyl group. For non-methylene interrupted (NMI) FAs, nomenclature of A:BΔX,Y,Z was used, where A and B are defined as above, and X, Y, and Z (if applicable) represent the position of the double bonds relative to the carboxylic acid group. NMI FAs are synthesized by herbivorous/detritivorous bivalves such as clams and mussels, sponges, and octopus (Barnathan 2009, Monroig et al. 2012), but are also found in predatory benthic invertebrates such as gastropods, chitons, sea urchins, and sea stars (Joseph 1982, Castell et al. 2004, Kraffe et al. 2004), and thus provide information on their importance in predator diets (e.g., Budge et al. 2007). Up to 76 FAME were identified by comparison of retention times with known standards (Nu Check Prep, Elysian, Minnesota, USA) or using GC-mass spectrometry (Appendix S2).

Carbon stable isotope ratios (expressed as δ^{13}C values in per mil – ‰) of individual FAME were analyzed by routing the effluent from a GC (Trace GC Ultra, Bremen, Germany) through a combustion interface (Finnigan GC combustion III, Bremen, Germany) to an isotope ratio mass spectrometer (IRMS; Thermo Finnigan Delta V, Bremen, Germany) at the Alaska Stable Isotope Facility, University of Alaska, Fairbanks, USA. The same GC column and method described above for FID analyses of FAME were used to separate the FAME for carbon stable isotope analysis using GC-IRMS (Budge et al. 2008, 2011, Wang et al. 2014). The δ^{13}C values from the individual FAMEs were calibrated using a standard mixture consisting of ethyl and methyl esters of 14:0, 16:0, 18:0, and 20:0 (supplied by Indiana University Stable Isotope Reference Materials), where the coefficient of determination (r^2) of the measured vs. expected relationship was >0.97. 16:0 and 18:0 FAME laboratory standards were analyzed after every 10 samples to track analytical error of the GC-IRMS system, which was ≤0.3‰ (representing 1 SD of 53 analyses of the 16:0 and 18:0 standards interspersed during the sample runs). All δ^{13}C values were reported relative to Vienna Pee Dee Belemnite (VPDB) using standard notation, where $\delta^{13}\text{C}\ (‰) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, and R is the corresponding ratio of ^{13}C/^{12}C.

Data analysis

Seals were harvested throughout the year, and months were grouped in two periods, the time of reduced feeding (April–August, referred to as spring–summer) and feeding (September–March, referred to as fall–winter), when diets of some species have been shown to differ (McLaren 1958, Lowry et al. 1980*a,b*, Cameron et al. 2010, Kelly et al. 2010, Boveng et al. 2013). Within species, diet estimates of ice seals based on stable isotope ratios and stomach contents can sometimes differ among age classes (Lowry et al. 1980*a,b*, Dehn et al. 2007, Quakenbush et al. 2011*a,b*), although there is evidence that FA profiles do not (Budge et al. 2007, Cooper et al. 2009). Nevertheless, we limited our analyses to samples from adult animals (≥5 yr) from locations in the Bering and Chukchi seas to remove any potential variation due to age. There is little evidence from stomach content or FA analyses of dietary differences between sexes in adult ice seals (Budge et al. 2007, Thiemann et al. 2007, Cooper et al. 2009, Quakenbush et al. 2011*a,b*).

Sample sizes in some cases were small, so only certain comparisons could be made within species. Because there is some indication that diets do differ between seals foraging in the Bering Sea compared to the Chukchi Sea (Lowry et al. 1980*a,b*, Quakenbush et al. 2009, 2011*a,b*), we compared a subset of bearded seal FA profiles for samples collected during spring–summer on Little Diomede (Bering Sea) and Point Hope (Chukchi Sea) in 2005, 2007, 2009, and 2010. Small sample sizes (Table 1; Appendix S1) did not allow us to compare FA profiles among sampling locations within years for the other seal species. Thus, we pooled all samples by season, sex, and location to make comparisons within species by year. To determine if the diets of ringed and bearded seals differed between the warm and cold periods, we pooled samples for warm years 2003–2005 for ringed seals and 2002–2005 for bearded seals, and from cold years 2007–2010 for both species. 2006 was not included in the warm or cold period because it is considered a transition year in the Bering Sea (Stabeno et al. 2012). To make comparisons among ice seal species, we pooled samples by species across all years, sexes, seasons, and locations. Although individuals of all species are highly mobile (e.g., Crawford et al. 2012), they are considered to be part of the same populations within the Bering and Chukchi seas (Boveng et al. 2009, 2013, Cameron et al. 2010, Kelly et al. 2010). Consequently, any inferences made are based at the population level for each species. Groups with only one sample were not included in the data analyses (Table 1).

FA data often violate the assumptions for parametric methods, therefore, we used non-parametric multivariate methods from PRIMER version 6 (PRIMER-E Ltd., 3

Meadow View, Lutton, Ivybridge, PL21 9RH, United Kingdom) (PRIMER-E; Clarke and Warwick 2001, Clarke and Gorley 2006) and a Kruskal–Wallis analysis of variance (ANOVA) to analyze FA data. We used Bray–Curtis similarity matrices and permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) to investigate the variation in FA compositions of ice seals, based on the 48 FAs present in proportions >0.1% (mean and 1 SD for each species are given in Appendix S2). We used distance-based redundancy analysis (dbRDA; McArdle and Anderson 2001) to visualize differences among FA profiles and assess the contribution of FAs to the variation observed among species, and non-metric multidimensional scaling (nMDS) plots to visualize differences between FA profiles during Bering Sea warm and cold years for ringed and bearded seals. FA data were standardized to 100% and $\log(X + 1)$-transformed prior to analysis to down weight the FAs present in higher proportions and increase the weighting of FAs present in lower proportions. We used Kruskal–Wallis ANOVA to test for differences of individual NMI FAs (20:2Δ5,11; 20:2Δ5,13; 20:3Δ5,11,14; 22:2NMID; 22:2Δ7,13, and 22:2Δ7,15) among species, and a Mann–Whitney U test to compare NMI FA levels between warm and cold years for ringed and bearded seals: NMID (non-methylene interrupted dienoic) FA is a form of NMI FA.

Because the $\delta^{13}C_{FA}$ data also violated assumptions for parametric statistics, we used the same non-parametric multivariate methods mentioned above to analyze $\delta^{13}C_{FA}$ data. Not all FAs were present in sufficient quantities to determine their respective $\delta^{13}C_{FA}$ values. $\delta^{13}C_{FA}$ values were determined for 14:0, 18:1n-11/9, 18:1n-7, and 18:2n-6 in all samples. Additionally, $\delta^{13}C_{FA}$ values could be determined for 16:0, 16:1n-7, 18:4n-3, 20:1n-11/9, 20:5n-3, 22:5n-3, and 22:6n-3 in all but eight samples (ringed seal $n = 1$, bearded seal $n = 4$, spotted seal $n = 2$, ribbon seal $n = 1$), therefore those samples were not used in the data analyses (Table 1). All FAs were resolved well by GC-FID, but co-elution of two pairs of FAs (18:1n-11 and 18:1n-9; 20:1n-11 and 20:1n-9) occurred on the GC-IRMS and are referred to as 18:1n-11/9 and 20:1n-11/9, respectively. We transformed the $\delta^{13}C_{FA}$ values for these 11 FAs into Euclidean distances and used PERMANOVA to investigate the variation in the $\delta^{13}C_{FA}$ values among species (ringed, bearded, spotted, ribbon seals), interannual variation within species (ringed, bearded, and spotted seals only), seasonal variation within species (ringed and bearded seals only), and any differences between warm and cold years (ringed and bearded seals only). We used a Kruskal–Wallis ANOVA to test for differences of individual $\delta^{13}C_{FA}$ values among species using STATISTICA version 12 (StatSoft, 2013). We set statistical significance, thus implied biological significance, at $\alpha = 0.10$.

We used a Bayesian multisource stable isotope mixing model (SIAR; Parnell et al. 2010) to estimate the proportional contribution of sympagic and pelagic FAs to ringed, bearded, and spotted seals in 2009, and ringed and bearded seals in 2010 (e.g., Wang et al. 2015). We used the $\delta^{13}C_{FA}$ values of particulate organic matter from sea ice (ice, i-POM) and from the water column (pelagic, p-POM) as proxies for sources of sympagic and pelagic FAs, since the composition of i-POM and p-POM we collected consisted mainly of algae (Wang et al. 2014). The $\delta^{13}C_{FA}$ values for i-POM and p-POM were generated from samples collected in the Bering Sea in 2009 and 2010 (Wang et al. 2014, 2015) and were used as the end member sources in our mixing models (Table 2a). Specifically, for ringed, bearded, and spotted seals sampled in 2009, we used mean i-POM and p-POM $\delta^{13}C_{FA}$ values of samples collected during ice melt between 14 April and 6 May 2009 (Wang et al. 2015) as sources in the mixing models for seals sampled in April–August 2009 (spring–summer 2009) and September 2009–March 2010 (fall–winter 2009). In 2010, we used the mean i-POM $\delta^{13}C_{FA}$ value from samples collected during maximum ice extent (13–28 March 2010; Wang et al. 2014) as the i-POM source for ringed and bearded seals sampled in April–August 2010. Also in 2010, p-POM was collected from maximum ice extent (13–28 March), ice melt (11 May–10 June 2010), and ice-free conditions (18 June–10 July 2010). The p-POM $\delta^{13}C_{FA}$ values for FAs 20:5n-3 and 22:6n-3 did not differ by ice conditions (Wang et al. 2014). Therefore, we averaged p-POM $\delta^{13}C_{FA}$ values for each FA across all ice conditions to use as the p-POM source in the model for ringed and bearded seals sampled in 2010. To test the use of these different FA markers as indicators of i-POM and p-POM, we ran two mixing models using (1) only the diatom FA 20:5n-3 and (2) 20:5n-3 and the flagellate

TABLE 2. The (a) $\delta^{13}C_{FA}$ values and (b) percentages of 20:5n-3 (diatom marker) and 22:6n-3 (flagellate marker) in i-POM and p-POM from 2009 and 2010.

Source	(a) $\delta^{13}C_{FA}$ values				(b) Percentage			
	20:5n-3		22:6n-3		20:5n-3		22:6n-3	
i-POM 2009	−26.5	3.0	−26.2	2.9	20.3	7.7	2.2	0.8
p-POM 2009	−29.7	1.3	−30.4	0.8	23.2	4.4	3.8	0.5
i-POM 2010	−26.5	2.8	−23.8	3.2	19.6	6.6	2.5	0.8
p-POM 2010	−29.7	1.7	−27.6	2.4	10.3	5.8	5.0	3.4

Notes: $\delta^{13}C_{FA}$ values were used as sources and the percentages were used as concentration dependencies in the SIAR stable isotope mixing models (mean and 1 SD).

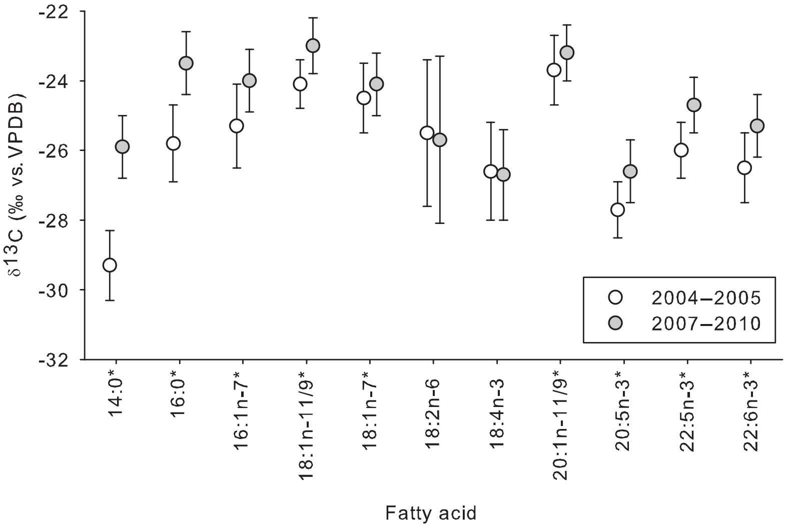

FIG. 2. $\delta^{13}C$ values for 11 fatty acids (FAs) in blubber of adult bearded seals in 2004–2005 (Bering Sea warm period; $n = 32$) and 2007–2010 (Bering Sea cold period; $n = 48$). Asterisks indicate FAs with a significant difference between seals collected in 2004–2005 and 2007–2010 (Mann–Whitney *U* test, $P < 0.07$). Sample sizes are given in Table 1. Symbols and whiskers represent mean ± 1 SD.

marker FA 22:6n-3 as sources of i-POM and p-POM. We used the diatom marker FA 20:5n-3 (e.g., Viso and Marty 1993) in the model because the algal composition in i-POM is typically dominated by diatoms (Horner 1985, Gradinger 2002, Arrigo et al. 2010). The presence of diatoms was also found in p-POM in 2010 (Wang et al. 2014). We also used the flagellate marker 22:6n-3 (e.g., Dalsgaard et al. 2003) in the model, because non-diatom phytoplankton, such as dinoflagellates, flagellates, and prymnesiophytes can be found in sea ice and the water column (Różanska et al. 2009, Moran et al. 2012). Trophic enrichment factors were assumed to be zero (Budge et al. 2008, 2011). Models were run with and without concentration dependencies for comparison (e.g., Wang et al. 2015; Table 2b). Results are presented as mean and 95% credibility interval (Bayesian confidence interval).

RESULTS

$\delta^{13}C_{FA}$ values of fatty acids

Comparisons within species

There was no difference in $\delta^{13}C_{FA}$ values between seasons for ringed seals (PERMANOVA $P = 0.56$) or bearded seals (PERMANOVA $P = 0.36$). The $\delta^{13}C_{FA}$ values of bearded seals from Bering Sea warm years 2004 and 2005 were different than the cold years 2007–2010 (PERMANOVA, see Appendix S3 for *P* values): specifically, the $\delta^{13}C_{FA}$ values for nine of the 11 FA (14:0, 16:0, 16:1n-7, 18:1n-11/9, 18:1n-7, 20:1n-11/9, 20:5n-3, 22:5n-3, and 22:6n-3) were lower in samples from the warm years than the cold years (Mann–Whitney *U*-test, $P < 0.07$; Fig. 2). Ringed seal $\delta^{13}C_{FA}$ values did not differ across years (PERMANOVA $P = 0.17$) or between the warm years and cold years (PERMANOVA $P = 0.58$). $\delta^{13}C_{FA}$ values of spotted seals collected during the fall–winter season differed among years (PERMANOVA $P = 0.03$).

Comparisons among species

Comparisons of $\delta^{13}C_{FA}$ values of 11 FAs showed that ringed, bearded, and spotted seals separated from each other in ordination space and that spotted and ribbon seals did not (PERMANOVA $P < 0.01$; Fig. 3). Bearded seals had higher $\delta^{13}C_{FA}$ values for all 11 FAs compared with ringed seals, and they had higher values than spotted seals for seven of the 11 FAs (16:1n-7, 18:1n-11/9, 18:1n-7, 18:2n-6, 18:4n-3, 20:1n-11/9, 22:5n-3; Kruskal–Wallis ANOVA $P < 0.01$; Fig. 4). Spotted seals had higher $\delta^{13}C_{FA}$ values of 14:0, 16:0, 18:1n-11/9, 18:4n-3, 20:5n-3, 22:5n-3, and 22:6n-3 than ringed seals, although $\delta^{13}C_{FA}$ of 18:1n-7 was higher in ringed seals (Kruskal–Wallis ANOVA $P < 0.02$; Fig. 4). $\delta^{13}C_{FA}$ values for spotted and ribbon seals collected during spring–summer 2003 were not different (PERMANOVA $P = 0.77$).

The results from two stable isotope mixing models (one using 20:5n-3, the other using 20:5n-3 and 22:6n-3) indicated that overall, bearded seals had the highest estimated contribution of i-POM in their diets (62–80%), followed by spotted seals (51–62%), then ringed seals (21–60%; Table 3). Concentration-dependent model results were similar to the results from the models that did not use source concentrations for seals in 2009 using 20:5n-3, and for seals in 2010 using 20:5n-3 and 22:6n-3 as sources of i-POM (Table 3). Concentration dependent model results for seals in 2009 using 20:5n-3 and 22:6n-3 as sources of i-POM were somewhat higher (between 7% and 10%) than the same model without concentration data (Table 3). In contrast, concentration-dependent model results for

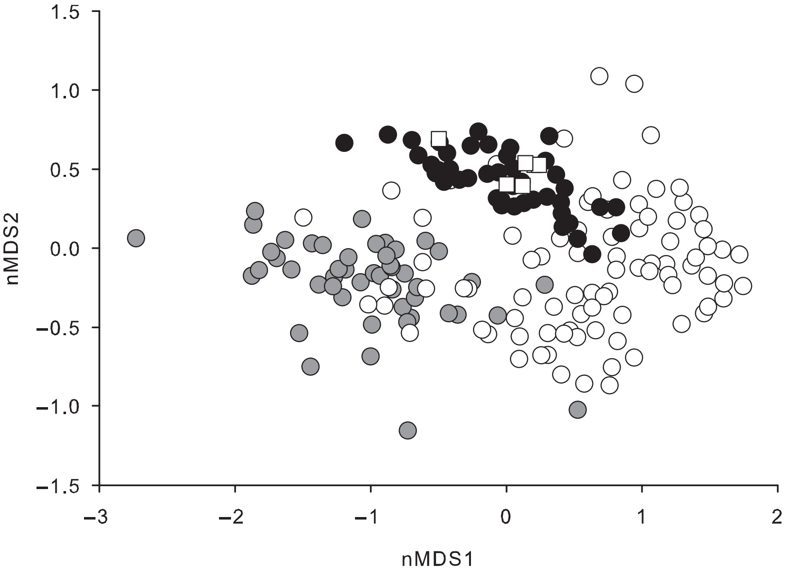

FIG. 3. Non-metric multidimensional scaling (nMDS) plot of the $\delta^{13}C_{FA}$ values of 11 fatty acids in blubber of adult ringed, bearded, spotted, and ribbon seals. Ringed seals are represented by gray circles, bearded seals are open circles, spotted seals are black circles, and ribbon seals are open squares. 2D stress = 0.07.

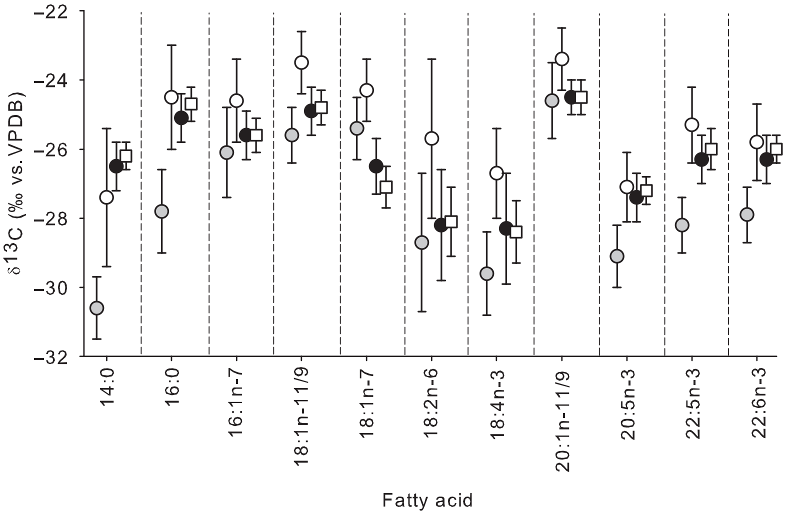

FIG. 4. $\delta^{13}C$ values for 11 fatty acids in blubber of adult ringed, bearded, spotted, and ribbon seals. Ringed seals are represented by gray circles, bearded seals are open circles, spotted seals are black circles, and ribbon seals are open squares. Samples are pooled by species. Sample sizes are given in Table 1. Symbols and whiskers represent mean ± 1 SD.

bearded seals in 2010 using only 20:5n-3 as a source of i-POM were somewhat lower (13%) than the results from the same model without concentration data (Table 3).

Fatty acid profiles

Comparisons within species

FA profiles did not differ between seasons (spring–summer vs. fall–winter) within species for which comparisons could be made (ringed seal: PERMANOVA $P = 0.31$ and bearded seal: PERMANOVA $P = 0.36$). There was some interannual variation in FA profiles of ringed, spotted, and bearded seals (ringed and spotted seal PERMANOVA $P = 0.01$, bearded seal PERMANOVA $P = 0.03$), but no clear patterns (Appendix S4). FA profiles pooled across years (2005, 2007, 2009, and 2010) of bearded seals collected near Little Diomede in the Bering Sea differed from profiles of animals collected near Point Hope in the Chukchi Sea ($P < 0.01$) and differed, or nearly so, between each individual year (PERMANOVA; see Table 4 for P values).

Table 3. Estimates of i-POM (%) contribution to adult ringed, bearded, and spotted seals during spring–summer (SS) and fall–winter (FW) in 2009 and 2010 from SIAR stable isotope mixing models.

	Concentration dependency (0)			Concentration dependency included		
2009 (20:5n-3)	Mean	Low 95% CI	High 95% CI	Mean	Low 95% CI	High 95% CI
Bearded seal SS	62	41	87	64	44	88
Ringed seal FW	24	2	47	26	3	50
Ringed seal SS	21	0	50	22	0	51
Spotted seal FW	51	32	72	54	35	74
2009 (20:5n-3, 22:6n-3)	Mean	Low 95% CI	High 95% CI	Mean	Low 95% CI	High 95% CI
Bearded seal SS	80	62	99	87	71	101
Ringed seal FW	42	25	59	50	26	69
Ringed seal SS	39	16	60	46	16	71
Spotted seal FW	62	47	77	72	56	87
2010 (20:5n-3)	Mean	Low 95% CI	High 95% CI	Mean	Low 95% CI	High 95% CI
Bearded seal SS	72	54	91	59	40	82
Ringed seal SS	47	6	85	43	3	83
2010 (20:5n-3, 22:6n-3)	Mean	Low 95% CI	High 95% CI	Mean	Low 95% CI	High 95% CI
Bearded seal SS	61	30	98	62	32	97
Ringed seal SS	60	47	74	60	46	75

Notes: Models used diatom marker 20:5n-3 and both 20:5n-3 and flagellate marker 22:6n-3 as sources of i-POM and p-POM. Results are shown for models that assumed no concentration dependency and for those that did, using concentrations from Table 2b. Sample sizes are given in Table 1. Mean and 95% credibility interval.

Table 4. Results of PERMANOVA analysis for adult bearded seal fatty acid profiles between Little Diomede and Point Hope in 2005, 2006, 2009, and 2010.

Year	*P*	Permutations
2005	**0.01**	998
2007	0.13	10
2009	0.12	126
2010	**0.01**	674

Notes: Values in bold type indicate significance at $\alpha < 0.10$. Permutations are the number of unique permutations.

Bearded seal and ringed seal FA profiles from samples pooled across warm years did not differ from samples pooled across cold years (bearded seal PERMANOVA $P = 0.26$, ringed seal PERMANOVA $P = 0.58$). There was little variation overall between values of NMI FAs in the warm and cold years for either ringed or bearded seals (Mann–Whitney *U* test; see Table 5a for *P* values; Fig. 5), although 20:2Δ5,11 differed in both species.

Comparisons among species

Variability in FA profiles was greater among species (PERMANOVA $P < 0.01$ for ringed, bearded, and spotted seals; Fig. 6) than within species. Spotted and ribbon seal FA profiles from spring–summer in 2003 were different (PERMANOVA $P = 0.07$; Fig. 6). Bearded seals had greater proportions of the NMI FA 20:2Δ5,11; 20:3Δ5,11,14; 22:2NMID; 22:2Δ7,13; and 22:2Δ7,15 compared to the other species (Fig. 7). Ringed, spotted, and ribbon seals did not differ from each other in the proportions of NMI FA, with the exception of 22:2Δ7,15, which was lower in ringed seals compared with spotted seals and 20:2Δ5,13 which as lower in ribbon seals compared with the other seal species. (Kruskal–Wallis ANOVA; see Table 5b for *P* values; Fig. 7). All FA data are provided in Appendix S2.

Discussion

$\delta^{13}C_{FA}$ *values of fatty acids*

Our isotope mixing models indicated that the strongest link with sea ice algae was for bearded seals (62–80% of FAs), followed by spotted seals (51–62%), then ringed seals (21–60%). Although we did not estimate the proportional contribution of POM sources to seals harvested from 2003 to 2008, due to the lack of POM data, our $\delta^{13}C_{FA}$ data for ribbon seals collected in 2003 suggested that their apparent consumption of sympagic FAs was similar to that of spotted seals in this study.

The most significant finding in our study was that the $\delta^{13}C_{FA}$ values in bearded seals sampled in the cold years were higher than in the warm years, indicating a greater contribution of sympagic FAs to their food web in the cold years. This would be expected because of the greater extent and duration of seasonal sea ice in the Bering Sea in cold years, assuming that production by ice algae is proportional to the extent and duration of sea ice. To our knowledge, this result provides the first empirical evidence of an ecosystem scale effect of a putative change in sympagic production in the Western Arctic.

The comparatively high $\delta^{13}C_{FA}$ values in bearded seals are a likely result of diets that typically include more benthic prey than diets of the other ice seals: benthic

Table 5. *P* values for the results from (a) Mann–Whitney *U* test comparing each non-methylene interrupted (NMI) fatty acid (FA) from Bering Sea warm and cold years for adult ringed and bearded seals and (b) Kruskal–Wallis ANOVA with multiple comparisons of NMI FAs among adult ringed, bearded, spotted, and ribbon seals.

	Ringed seal	Bearded seal
(a) NMI FA		
20:2Δ5,11	**0.01**	**0.02**
20:2Δ5,13	0.41	1.00
20:3Δ5,11,14	0.86	0.14
22:2NMID	0.28	0.85
22:2Δ7,13	0.69	0.64
22:2Δ7,15	0.90	0.60

(b)	Ringed seal	Bearded seal	Spotted seal
20:2Δ5,11			
Bearded seal	**<0.01**		
Spotted seal	0.13	**0.04**	
Ribbon seal	1.00	**0.01**	1.00
20:2Δ5,13			
Bearded seal	1.00		
Spotted seal	1.00	0.89	
Ribbon seal	**<0.01**	**<0.01**	**<0.01**
20:3Δ5,11,14			
Bearded seal	**<0.01**		
Spotted seal	1.00	**<0.01**	
Ribbon seal	0.32	**<0.01**	0.26
22:2NMID			
Bearded seal	**<0.01**		
Spotted seal	0.28	**<0.01**	
Ribbon seal	0.26	**<0.01**	1.00
22:2Δ7,13			
Bearded seal	**<0.01**		
Spotted seal	1.00	**<0.01**	
Ribbon seal	1.00	**<0.01**	1.00
22:2Δ7,15			
Bearded seal	**<0.01**		
Spotted seal	**<0.01**	**<0.01**	
Ribbon seal	1.00	**<0.01**	0.14

Note: Values in bold type indicate significance at $\alpha < 0.10$.

organisms commonly have higher $\delta^{13}C$ values than pelagic organisms (e.g., Hobson et al. 2002). In the case of bearded seal food webs, tight sympagic-benthic coupling in the Arctic and efficient consumption and assimilation of ice algae by benthic fauna (McMahon et al. 2006, Gradinger 2009) is a likely cause of the higher $\delta^{13}C$ values in benthic prey. An additional effect of bacterial and meiofaunal processes in isotopic enrichment of benthic organisms (McConnaughey and McRoy 1979) is possible but cannot be evaluated. Consumption of microphytobenthos, that also can be more enriched in ^{13}C than pelagic phytoplankton (France 1995), by benthic prey is probably not important, since productivity of microphytobenthos in the Arctic is negligible compared to that of pelagic and sympagic phytoplankton except in very shallow nearshore waters (Horner and Schrader 1982, Glud et al. 2009).

Ringed seals had the lowest apparent consumption of sympagic FAs, which was not expected considering their reliance on Arctic cod (McLaren 1958, Lowry et al. 1980*b*, Dehn et al. 2007, Quakenbush et al. 2011*a*) that at times and places feed extensively on sympagic amphipods (Lowry and Frost 1981*a*, Lønne and Gulliksen 1989, Renaud et al. 2012). However, the ringed seals we sampled presumably had been feeding in the southern Chukchi and Bering seas (all were harvested between Sishmaref and Hooper Bay; Fig. 1), where diets of Arctic cod may have been dominated by other taxa of invertebrates that were not as directly associated with under ice habitat and sympagic production. That is, Arctic cod diets in spring in the northern Bering Sea, where water column primary production is seasonally very high with tight pelagic-benthic coupling (Springer and McRoy 1993, Grebmeier et al. 2006), consisted of benthic gammarid amphipods, crangonid and hippolytid shrimp, and mysids (Lowry and Frost 1981*b*). It is also likely that ringed seals in the Bering Sea were foraging on species other than, or in addition to, Arctic cod. Lowry et al. (1980*a*) found that ringed seals in the southern Chukchi and northern Bering seas in spring–summer fed primarily on saffron cod (*Eleginus gracilis*) and pandalid, hippolytid, and crangonid shrimp that may not be tightly coupled to sympagic carbon.

The higher apparent consumption of sympagic FAs by spotted seals than by ringed seals also was not expected, since throughout the year spotted seals feed primarily on a variety of pelagic and demersal fishes (Lowry and Frost 1981*a*, Dehn et al. 2007) that overall are not known to be associated with sympagic food webs. Unless that assumption is wrong, then the higher $\delta^{13}C_{FA}$ values in spotted seals than in ringed seals may be an artifact of the timing and location of sampling. That is, the two species may have been foraging in regions very distant from each other, with different ambient $\delta^{13}C$ values. Lower bulk $\delta^{13}C$ values from the Beaufort Sea compared with continental shelf waters of the Bering and Chukchi seas were reported by Schell et al. (1998) and a similar pattern has been detected in zooplankton and benthic fauna from the southeast Bering Sea to the eastern Beaufort Sea (Dunton et al. 1989, Saupe et al. 1989, Schell et al. 1998). Also, all but one of the spotted seals in 2009 were collected in September and October from Shishmaref in the southern Chukchi Sea, while ringed seals in 2009 were collected during fall–winter and spring–summer at locations south of Shishmaref (Little Diomede, Savoonga, and Hooper Bay) in the Bering Sea. Thus, spotted seals likely had been foraging in areas with higher ambient $\delta^{13}C$ values than ringed seals, which could inflate the estimates of sympagic FAs in spotted seals relative to ringed seals. This explanation is likely if $\delta^{13}C$ values of FAs show a similar trend to bulk $\delta^{13}C$. Feeding in areas where prey have lower $\delta^{13}C$ values would result in a

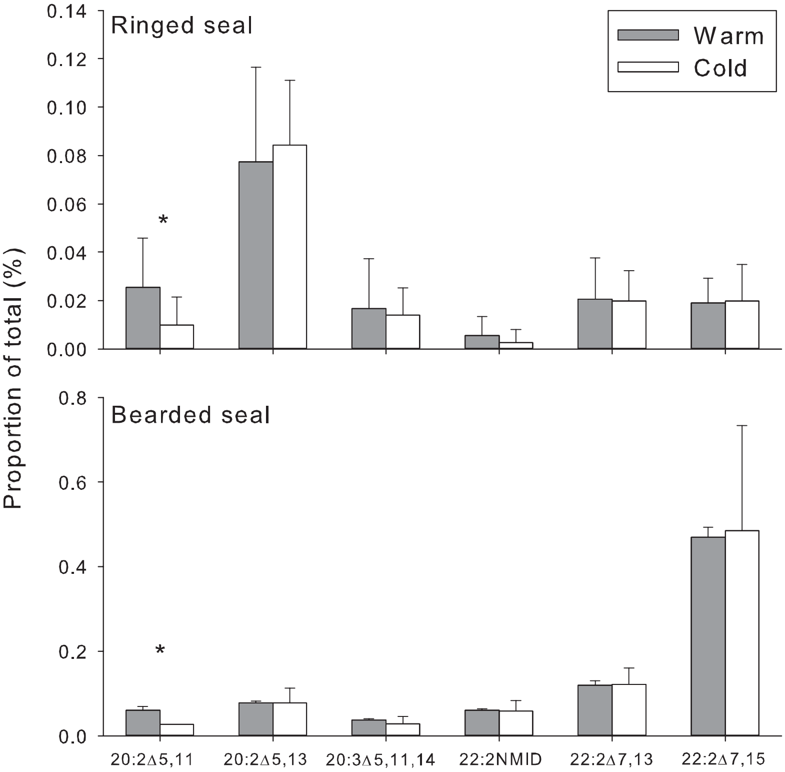

FIG. 5. Proportions of non-methylene interrupted (NMI) fatty acids (FAs) found in blubber of adult ringed and bearded seals during recent warm and cold years in the Bering Sea (Stabeno et al. 2012). NMI FAs with an asterisk indicate a significant difference between warm and cold years in the Bering Sea (Mann–Whitney *U* test, $P < 0.01$). Bars and whiskers represent mean + 1 SD.

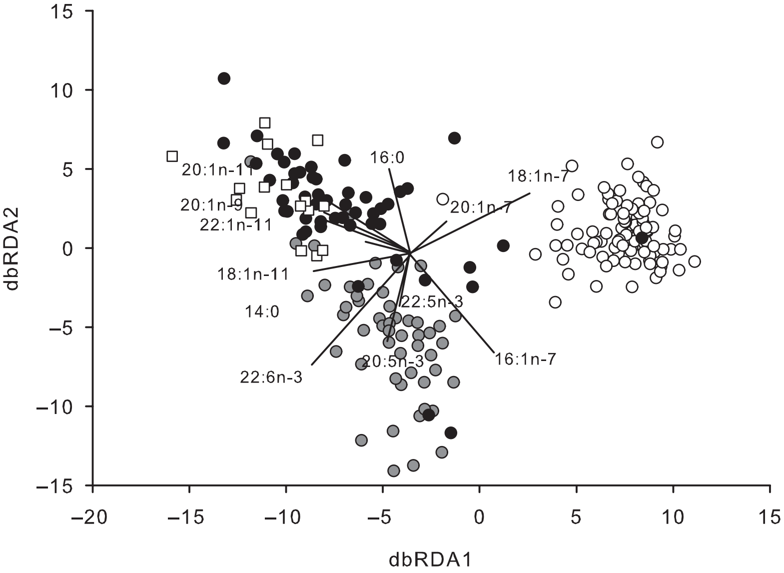

FIG. 6. Biplot of the distance-based redundancy analysis (dbRDA) relating the variability of fatty acid (FA) composition of adult ringed, bearded, spotted, and ribbon seals. Ringed seals are represented by gray circles, bearded seals are open circles, spotted seals are black circles, and ribbon seals are open squares. The first dbRDA axis explained 57.1% and 57.4% of the fitted and total variation, respectively. The second dbRDA axis explained 18.5% and 18.7% of the fitted and total variation, respectively. Vectors point toward the direction of maximum change. Key FAs that are significantly correlated with dbRDA axes are shown (multiple correlation >0.20). Sample sizes are given in Table 1.

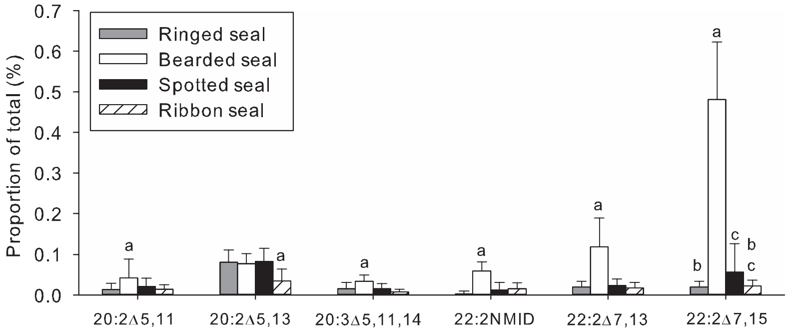

FIG. 7. Proportions of non-methylene interrupted fatty acids (NMI FAs) in blubber of adult ringed, bearded, spotted, and ribbon seals. For each NMI FA, groups with different letters are significantly different from each other (Kruskal–Wallis ANOVA, $P < 0.04$). Sample sizes are given in Table 1. Bars and whiskers represent mean + 1 SD.

lower estimated contribution of sea ice algae, as seen in ringed seals from Ulukhaktok, Canada (lower bulk $\delta^{13}C$ values from foraging in the eastern Beaufort Sea) compared to those from Barrow, Alaska (higher bulk $\delta^{13}C$ values from foraging in the Chukchi Sea; Dehn et al. 2007).

Our results differ from those of Budge et al. (2008) in that their estimate of the contribution of sympagic FAs to bearded and ringed seals harvested in July 2002 at Barrow, based on $\delta^{13}C_{FA}$ values of the diatom FA marker 20:5n-3, was lower (bearded seals: −25% to 23%; ringed seals: −5% to 12%) than ours (bearded seals: 59% to 72%, ringed seals: 21% to 47%). One possible explanation is that carbon sources to the food webs of the seals differed between the two studies, with diets in 2002 having been less connected to ice algae than those in 2009. This explanation could apply if seals sampled at Barrow in 2002 had wintered in the Bering Sea, when water temperature was much higher and sea ice was much lower than in 2009 (Stabeno et al. 2012) and sympagic production was arguably less. Another explanation again invokes the geographic gradient in ambient $\delta^{13}C$: all else being equal, $\delta^{13}C_{FA}$ values of seal prey in the Bering Sea would be expected to be higher than in the Chukchi and Beaufort seas near Barrow.

Our estimates of the proportional contribution of sympagic FAs to ice seals seem to be high when the ratio of sea ice algae production to total primary production is considered. In both the Bering and Chukchi seas, annual production by water column phytoplankton in any year is much higher than production by sea ice phytoplankton. For instance, the proportion of the total primary production originating from sea ice algae in the Bering Sea has been estimated to be as low as 3% (McRoy and Goering 1976), with a possible upper limit of 30% (R. R. Gradinger, *unpublished data*). Less is known about production dynamics on the Chukchi Sea shelf, but recent evidence suggests that water column primary production may be much higher than previously estimated (Arrigo 2012, 2014). If the amount of sea ice algae production is a small fraction of water column algae production, then how is it possible to have estimates of sympagic FA in upper trophic level consumers that are as high as those we estimated?

One plausible explanation is that some of the assumptions we made when using the SIAR model may have introduced biases in the estimates. We assumed that the proportions of each FA used in the model were present in i-POM and p-POM in similar quantities (Phillips and Koch 2002). However, the proportions of individual FAs often vary between primary production sources, which could skew the estimates of the contributions of i-POM and p-POM to a consumer toward one source. For example, the proportions of 20:5n-3 in i-POM and p-POM in 2009 differed by only about 3%, while in 2010 the proportion in i-POM was 10% higher than in p-POM (20% versus 10%). That difference may explain why the model estimate of i-POM FAs in bearded seals in 2010, using only 20:5n-3 as a source without concentration data, was a similar amount higher (13%) than the estimate that incorporated concentration data. However, the estimates for ringed seals in 2010, using the same model parameters, differed by just 4%. Thus, the potential error introduced by using one approach or another was small compared to the magnitude of the estimates of i-POM in the seals. Further work with modeling is required to resolve this possibility.

Isotopic fractionation associated with the metabolism of FAs also could influence the model estimates. Fractionation due to modification through chain elongation and desaturation would likely result in at least slightly higher $\delta^{13}C_{FA}$ values (Monson and Hayes 1982), which could bias our estimates toward a higher contribution of sympagic FAs. However, Budge et al. (2011) found no isotopic discrimination of those FAs between the diet and adipose tissue of two species of marine ducks (*Polysticta stelleri* and *Somateria fischeri*). Furthermore, in marine environments where long-chain essential polyunsaturated FAs such as 20:5n-3 and 22:6n-3 are abundant, there is strong evidence that the activity level of enzymes responsible for de novo synthesis of these FAs in marine vertebrates is minor (Tocher 2003). Thus, we assumed that isotopic fractionation associated with the metabolism of these FAs is negligible. Further work is needed to resolve this possibility as well and to understand processes that drive the dynamics of FAs and isotopes in algae and food webs.

Fatty acid profiles

Our results from FA analysis alone corroborate previous findings that the diets of ringed, bearded, and spotted seals differ and that there is apparently little niche separation between spotted and ribbon seals. The comparatively high amount of NMI FAs in bearded seals supports the inference from $\delta^{13}C_{FA}$ data that they consume proportionally more benthic invertebrates (e.g., bivalves and/or gastropods) than the other species of ice seals. Our results are similar to those based on FAs reported by Cooper et al. (2009) for ice seals sampled in 2003 from Little Diomede, which indicates that despite the recent environmental changes in the Bering Sea, the diet separation Cooper et al. (2009) found among ringed, bearded, and spotted seals in warm years persisted in subsequent cold years.

Ringed and bearded seal FA profiles did not vary between the spring–summer and fall–winter months. These results are consistent with results from stomach content analysis of bearded seals harvested between 1960 and 2009 (Quakenbush et al. 2011*b*) and with the lack of a consistent seasonal pattern in the $\delta^{13}C$ and $\delta^{15}N$ values of ringed seal claws (Carroll et al. 2013). In contrast, estimates of ringed seal diets based on stomach contents have indicated pronounced seasonal variability (Lowry et al. 1980*a*, Quakenbush et al. 2011*a*). The differences between the two sets of studies may be due to the different temporal scales that the analyses represent: stomach contents provide information on recent feeding, while blubber FA profiles reflect an average of prey acquired over weeks to several months (Iverson et al. 2004, Nordstrom et al. 2008, Tollit et al. 2010), and stable isotopes from claw sheaths incorporate seasonal and interannual changes in diet and can reflect dietary information for up to 10 years (McLaren 1958, Ferreira et al. 2011, Carroll et al. 2013). Thus, snapshots of the recent feeding of ringed seals from stomach content analyses may have been more variable between seasons than diets integrated over longer times inferred from FA profiles and stable isotopes.

FA profiles of bearded seals at Little Diomede in the Bering Sea and Point Hope in the Chukchi Sea revealed significant differences in diet. The diets of bearded seals, and ice seals in general, can be highly variable, likely due to geographic differences in prey assemblages (Lowry et al. 1980*b*, Antonelis et al. 1994; and reviewed in Boveng et al. 2009, 2013, Cameron et al. 2010, and Kelly et al. 2010). In this case, oceanographic processes across the northern Bering–Chukchi continental shelf have been shown to affect patterns of pelagic and benthic community composition (Springer et al. 1996, Grebmeier 2012) that would be expected to be reflected in characteristics of food webs supporting bearded seals. The geographic difference further indicates that despite the high mobility of bearded seals, little overlap occurred in the winter foraging areas of the seals from the two locations.

When bearded seal and ringed seal FA data were pooled by species across all warm years and cold years, they were not different between the thermal regimes. This indicates that prey fields were not altered sufficiently by this large multiyear environmental fluctuation to cause change in bearded and ringed seal diets.

Conclusions

The pairing of information from $\delta^{13}C_{FA}$ ratios and FA profiles linked ice seals with both sympagic and pelagic carbon sources in the marine food web. This supports earlier evidence that molecular and isotopic biomarkers of these sources of organic matter input at the base of the food web in the Bering Sea are recorded in both pelagic and benthic food webs (Budge et al. 2008, Graham et al. 2014, Wang et al. 2015). However, our understanding of mechanisms governing the movement of FAs derived from sympagic and pelagic sources through food webs to higher trophic levels is hampered by our incomplete understanding of food web production processes in these systems. We have only rough estimates of the amount of annual production of ice algae, and there are numerous trophic connections between primary producers and higher trophic levels about which we have only a general understanding. Even less is known about factors that affect those connections, e.g., the strength of pelagic and benthic coupling to pelagic phytoplankton and ice algae, the importance of trophodynamic phasing, and how variability is expressed in species such as ice seals.

Although there are several caveats in using FA and compound-specific isotope analysis, this study demonstrated the utility of these approaches and provided unprecedented insight into carbon sources in Arctic food webs in relation to recent environmental changes in the Bering Sea. Specifically, our results provided compelling evidence that ice algae are important in ice seal food webs and that community and food web characteristics changed between the recent environmentally warm and cold periods in the Bering Sea. Differences in the relative input of sympagic and pelagic carbon to food webs, based on $\delta^{13}C_{FA}$ ratios, could have resulted from changes in the thermal environment, variations in bulk primary production, or alterations in trophodynamic phasing that is important to primary consumers. But, unless the quality or quantity of ice seal prey was affected by changing proportions of sympagic and pelagic carbon input, we surmise that there was minimal effect on life history traits (such as growth, reproduction, and survival) of the seals.

The comparisons we made in this study are in relation to environmental changes that occurred over a span of nine years: a four-year warm period followed by a four-year cold period, with a transition year between them. Comparisons across longer time spans would improve our understanding about how ice seal food webs respond to changes in the marine environment and carbon sources. Continuing to monitor ice seal diets and quantify the contributions of sympagic and pelagic organic matter to them using our approach and other tools, e.g., analysis of highly branched isoprenoids to estimate the contribution of organic matter derived from ice algae to Arctic food webs (Brown et al. 2014), will help us understand the degree to which climate change may alter ecosystem function in the Bering Sea, anticipate possible effects on ice seals and other upper trophic level species, and devise appropriate ecosystem based management strategies for them as needed.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1890/14.2421/suppinfo

DATA AVAILABILITY

Data associated with this paper have been deposited in the NSF Arctic Data Center: https://www.aoncadis.org/project/tracking_the_seasonal_contribution_of_algal_fatty_acids_to_the_arctic_marine_system.html