Polar Biol (2009) 32:1137–1145
DOI 10.1007/s00300-009-0614-5

ORIGINAL PAPER

Resource partitioning by sympatric pagophilic seals in Alaska: monitoring effects of climate variation with fatty acids

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Received: 8 April 2008 / Revised: 26 August 2008 / Accepted: 28 February 2009 / Published online: 26 March 2009

Abstract Four species of pagophilic phocid seals in the Western Arctic—bearded (*Erignathus barbatus*), ringed (*Phoca hispida*), ribbon (*Phoca fasciata*), and spotted (*Phoca largha*)—are particularly vulnerable to arctic warming trends. Documenting diet composition over time is one way in which the flexibility of a species, in the face of broad ecosystem changes, can be measured. Because the fatty acid (FA) composition of depot lipids has long been known to reflect diet, we analysed the FA composition of blubber samples collected from bearded ($n = 30$), ringed ($n = 15$), ribbon ($n = 32$) and spotted seals ($n = 24$). All animals were taken near Little Diomede Island in May and June 2003, providing a unique opportunity to study interspecies differences with minimal effects of spatial and temporal variation. Bearded seal FA composition was significantly different from all other seals ($P < 0.001$ in all cases), ringed seal FA composition was significantly different from that of both ribbon and spotted seals ($P < 0.001$), but ribbon and spotted seal FA compositions could not be distinguished from each other. Overall, the blubber FA compositions of ribbon, ringed and spotted seals implied diets dominated by pelagic prey. Inferences we made about current diets of bearded and ringed seals suggest that certain prey important to them in this area in the 1970s remain important today, despite notable changes in the ecosystem. We believe that blubber FA analysis will be a useful tool in assessing the response of ice-associated pinnipeds and their ecosystem to changes associated with arctic warming.

Keywords Lipid · Trophic studies · Climate change · Ice seal · Blubber fatty acid

Introduction

Rapid warming of the Western Arctic is resulting in significant reductions in sea ice cover, thickness, and persistence, due to snow and sea-ice albedo feedback processes (Serreze et al. 2000; Comiso 2002; Rigor and Wallace 2004), as well as broad shifts in distributions of organisms that are important prey of numerous higher trophic level predators (Overland and Stabeno 2004; Grebmeier et al. 2006; Mueter and Litzow 2008). Among these predators are four species of pagophilic ("ice-loving") phocid seals—bearded (*Erignathus barbatus*), ringed (*Phoca hispida*), ribbon (*Phoca fasciata*), and spotted (*Phoca largha*) seals—that depend on sea ice for reproduction, molting, and foraging for much or all of the year (Fay 1974). Thus, ice-associated seals are particularly vulnerable to warming trends because of the direct effect of a reduction in sea-ice habitat, as well as the generalized effect of ecosystem changes that alter the spatial and temporal patterns of prey availability.

Both sea ice habitat and foraging strategies vary among these seals (Burns 1981a; Lowry et al. 2000; Simpkins et al. 2003). Bearded seals are restricted to waters of about 130 m depth or less because they are primarily benthic foragers. They feed mainly on crabs, clams, shrimps and fish such as eelpouts and sculpins, but demersal and pelagic cods and capelin (*Mallotus villosus*) also can be important

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prey (Lowry et al. 1980a; Burns 1981b; Antonelis et al. 1994; Dehn et al. 2007). For much of the year, the main prey of ringed seals appears to be Arctic cod (*Boreogadus saida*) but during spring and summer, invertebrates or other fish species can constitute the majority of the diet (Lowry et al. 1980b; Dehn et al. 2007). Diets of ribbon and spotted seals are similar—Arctic cod is considered the primary prey of both species, with ribbon seals also having been found to consume walleye pollock (*Theragra chalcogramma*) and spotted seals having been found to consume several species of fishes such as pollock, Pacific herring (*Clupea pallasii*) and capelin, as well as octopus in spring (Frost and Lowry 1980; Bukhtiyarov et al. 1984; Lowry et al. 2000). Precise information on prey resource overlap or partitioning between these ice seals has been difficult to obtain, however, because samples have been taken in various seasons, years and locations.

Differences between the species in prey and habitat selection will likely cause them to be uniquely affected by Arctic warming, the loss of sea ice and any resultant ecosystem shifts. One way to assess their flexibility to accommodate broad ecosystem changes is by studying diet composition over time. Previous studies of ice seal diets in Alaska have been based on stomach content analysis; however this method has several biases (Jobling and Breiby 1986; Dellinger and Trillmich 1988). An alternative method for estimating diets is through the use of dietary fatty acids (FA), which have long been known to influence the FA composition of the depot lipids of consumers (Fraser et al. 1989; Raclot et al. 1998; Kirsch et al. 2000), and the analysis of blubber FA composition provides an alternative method of studying pinniped diet (Iverson 1993; Iverson et al. 2004). A primary advantage of that approach, which we employed in this study, is that it provides longer-term information about the diet than the traditional stomach or scat analyses, which only provide information about an animal's most recent meals. This is particularly relevant to ice seals sampled in spring, a time of reduced feeding when stomachs often contain few prey remains (e.g., Shustov 1965; Frost and Lowry 1980; Burns 1981a).

West et al. (1979) presented blubber FA compositions of these ice seals, but interpretations of the data were severely limited due to their small sample size ($n = 8$), a 7-month sample collection period, and collection locations at several oceanographically distinct areas ranging from the Bering Sea to the Beaufort Sea. In our study, much larger numbers of animals were sampled in a small geographic area near Little Diomede Island in the Bering Strait region of Alaska and over a short time period in May and June 2003, providing a unique opportunity to assess interspecies differences and similarities with minimal interference from spatial and temporal variation.

A primary objective of this project was to assess changes in the diets of these four species over time. This required the comparison of past diet estimates based on stomach contents and very limited FA data with current qualitative diet analyses using only FA data. Because diet estimation using FA is a relatively new technique, comparison of our results to those from previous studies using stomach content analysis was necessary to determine whether diet changes have occurred over the time that has elapsed between studies (i.e., sufficient FA data were not collected in the past to rely exclusively on that source for diet information). In the future, we anticipate the use of FA data for diet estimation as a long-term monitoring method to study the influence of climate change on these mammals. Thus, another objective of this work was to establish a FA data set for future comparisons.

Materials and methods

Sample source and extraction

Blubber samples from 101 ice seals (bearded $n = 30$; ringed $n = 15$; ribbon $n = 32$; spotted $n = 24$) were collected from the Native subsistence harvest near Little Diomede Island, AK (65.75 N, 168.95 W) during May and June 2003. Each sample was full thickness (from skin to muscle, approximately 2–3 cm in depth), ~100–300 g each, and was collected within 24 h of death. Samples from all four species included both sexes and adult and sub-adult age classes, but this information was not known for approximately 25% of the samples. Samples were frozen at –20°C until analyzed. A longitudinal slice (1–2 g) of blubber was sub-sampled, and skin and muscle were removed. Lipids were quantitatively extracted with chloroform and methanol and FA methyl esters (FAME) were prepared from the extracted lipid using H_2SO_4 in methanol (Budge et al. 2006).

Chromatography

FAME were analyzed in duplicate using temperature-programmed gas chromatography on a Perkin Elmer Autosystem II Capillary gas chromatograph (GC) with a flame ionization detector using a polar column (Agilent Technologies, DB-23; 30 m × 0.25 mm ID) according to Budge et al. (2006). Up to 66 FAME were routinely identified according to Iverson et al. (1997) and are reported as weight percent of total FA identified. Unusual non-methylene-interrupted (NMI) FA were identified using silver nitrate chromatography and GC-mass spectrometry as described in Budge et al. (2007).

Statistics

To investigate the variation in blubber FA composition among and within species by age and sex, Bray–Curtis similarity matrices (Bray and Curtis 1957) were calculated on all FA present at proportions >0.1%. Differences were visualized through ordination of samples using non-metric multidimensional scaling (MDS). The adequacy of the MDS ordination was verified using the results of a cluster analysis. An analysis of similarity (ANOSIM, Clarke 1993) was performed and significant differences in FA profiles were identified using *R* values. A similarity percentages routine (SIMPER) was then used to determine the FA contributing to the differences. The above analyses were performed using the PRIMER 6 statistical package (Primer-E Ltd; Clarke and Warwick 2001; Clarke and Gorley 2006). Species mean values for total n-3 FA concentration were compared using a one-way ANOVA in SPSS 10. FA data were transformed using an arcsine square root function prior to statistical analysis.

Results

The FA composition of blubber lipids from all seals are presented in Table 1. ANOSIM, using sex and age as factors, did not indicate any significant intraspecific differences among FA profiles; thus for each species FA data were treated as a single group in subsequent analyses. ANOSIM also indicated an overall difference in FA composition between the four seal species ($R = 0.71$, $P = 0.001$). Pair-wise ANOSIM indicated that bearded seal FA composition was significantly different from all other seals ($P < 0.001$ in all cases). Ringed seal FA composition was also significantly different from that of both ribbon and spotted seals ($P < 0.001$), but ribbon and spotted seal FA compositions could not be distinguished from each other.

MDS ordination of samples clearly showed that bearded and ringed seals were separated from all other species, but that ribbon and spotted seals were too similar to be separated from each other (Fig. 1). The groupings superimposed on the ordination plot represent 90% similarity based on cluster analysis and show an excellent agreement between the two techniques. The small number of obvious outliers present in Fig. 1 could have possibly resulted from mislabeling or misidentification in the field.

SIMPER analysis identified the FA that were contributing most strongly to the above differences, and Fig. 2 presents the blubber composition of these important FA. The much higher level of n-7 FA in the bearded seal, specifically 18:1n-7 and 20:1n-7, compared to the other seals, was central to its differentiation. In addition, bearded seals had greater proportions of 20:4n-6 as well as all NMI FA (Table 1). The low proportions of n-9 and n-11 monounsaturated FA (MUFA) in bearded seals further differentiated them from the ribbon and spotted seals. Differences

Table 1 Proportions of FA (mean ± SE, expressed as mass percent of total FA) in blubber of four species of ice-associated seals

	Bearded Seals *n* = 30	Ringed Seals *n* = 15	Ribbon Seals *n* = 32	Spotted Seals *n* = 24
Saturated				
14:0	2.93 ± 0.07	3.80 ± 0.19	4.34 ± 0.12	4.28 ± 0.13
15:0	0.39 ± 0.01	0.25 ± 0.02	0.25 ± 0.01	0.26 ± 0.01
16:0	9.30 ± 0.32	6.39 ± 0.33	6.91 ± 0.34	8.51 ± 0.34
i-17:0	0.30 ± 0.01	0.13 ± 0.02	0.11 ± 0.00	0.13 ± 0.00
17:0	0.29 ± 0.02	0.10 ± 0.02	0.09 ± 0.00	0.11 ± 0.01
18:0	1.30 ± 0.07	0.71 ± 0.08	0.87 ± 0.05	0.98 ± 0.06
Subtotal	14.51 ± 0.39	11.39 ± 0.50	12.57 ± 0.43	14.27 ± 0.46
Monounsaturated				
14:1n-5	0.77 ± 0.07	1.24 ± 0.07	1.26 ± 0.06	0.86 ± 0.06
16:1n-11	0.47 ± 0.02	0.58 ± 0.03	0.52 ± 0.02	0.49 ± 0.02
16:1n-9	0.33 ± 0.01	0.47 ± 0.03	0.33 ± 0.01	0.41 ± 0.02
16:1n-7	20.10 ± 0.43	18.87 ± 1.06	14.33 ± 0.57	14.21 ± 0.56
17:1	0.61 ± 0.02	0.32 ± 0.05	0.32 ± 0.01	0.32 ± 0.01
18:1n-11	0.49 ± 0.07	2.32 ± 0.34	1.96 ± 0.16	1.83 ± 0.16
18:1n-9	16.03 ± 0.51	15.94 ± 1.05	22.94 ± 0.81	21.93 ± 0.49
18:1n-7	9.28 ± 0.31	5.15 ± 0.36	4.47 ± 0.13	4.95 ± 0.16
18:1n-5	0.57 ± 0.01	0.59 ± 0.02	0.53 ± 0.01	0.56 ± 0.02
20:1n-11	2.16 ± 0.21	2.31 ± 0.36	6.91 ± 0.47	4.70 ± 0.35
20:1n-9	2.04 ± 0.19	4.72 ± 0.54	5.64 ± 0.31	6.85 ± 0.43
20:1n-7	2.43 ± 0.14	0.49 ± 0.12	0.34 ± 0.02	0.44 ± 0.03
22:1n-11	0.39 ± 0.08	1.04 ± 0.24	3.39 ± 0.36	2.27 ± 0.35
22:1n-9	0.22 ± 0.02	0.26 ± 0.05	0.48 ± 0.04	0.35 ± 0.04
Subtotal	55.90 ± 0.81	54.29 ± 1.16	63.41 ± 0.65	60.16 ± 0.79
Polyunsaturated				
16:2n-4	0.16 ± 0.01	0.14 ± 0.01	0.22 ± 0.01	0.16 ± 0.01
16:3n-6	0.42 ± 0.01	0.58 ± 0.03	0.49 ± 0.02	0.50 ± 0.02
16:3n-4	0.22 ± 0.01	0.28 ± 0.02	0.23 ± 0.02	0.26 ± 0.01
16:4n-1	0.32 ± 0.02	0.34 ± 0.04	0.33 ± 0.03	0.32 ± 0.02
18:2n-6	0.89 ± 0.03	0.82 ± 0.04	1.13 ± 0.03	0.94 ± 0.02
18:2n-4	0.27 ± 0.01	0.15 ± 0.01	0.12 ± 0.00	0.13 ± 0.00
18:3n-4	0.23 ± 0.01	0.12 ± 0.01	0.11 ± 0.01	0.10 ± 0.00
18:3n-3	0.24 ± 0.02	0.37 ± 0.02	0.48 ± 0.02	0.36 ± 0.01
18:4n-3	0.63 ± 0.03	0.89 ± 0.04	0.93 ± 0.05	0.81 ± 0.03
18:4n-1	0.27 ± 0.01	0.18 ± 0.01	0.19 ± 0.01	0.14 ± 0.01
20:2n-6	0.36 ± 0.01	0.18 ± 0.02	0.18 ± 0.01	0.18 ± 0.01
20:4n-6	1.19 ± 0.05	0.57 ± 0.08	0.36 ± 0.02	0.47 ± 0.03
20:4n-3	0.41 ± 0.02	0.38 ± 0.01	0.54 ± 0.01	0.32 ± 0.01
20:5n-3	8.76 ± 0.29	9.07 ± 0.50	5.12 ± 0.25	5.38 ± 0.38
21:5n-3	0.54 ± 0.02	0.44 ± 0.02	0.41 ± 0.01	0.38 ± 0.01
22:4n-6	0.25 ± 0.01	0.10 ± 0.02	0.05 ± 0.01	0.09 ± 0.01
22:5n-6	0.26 ± 0.01	0.11 ± 0.01	0.09 ± 0.01	0.12 ± 0.01
22:5n-3	4.20 ± 0.13	6.01 ± 0.42	3.43 ± 0.18	4.48 ± 0.18
22:6n-3	6.33 ± 0.14	11.00 ± 0.60	7.04 ± 0.23	7.84 ± 0.25
Subtotal	25.94 ± 0.47	31.72 ± 1.39	21.46 ± 0.63	22.97 ± 0.79
Non-methylene interrupted				
20:2Δ5,11	0.16 ± 0.01	0.02 ± 0.01	0.01 ± 0.00	0.03 ± 0.00
20:2Δ5,13	0.10 ± 0.01	0.02 ± 0.01	0.02 ± 0.00	0.03 ± 0.00

Table 1 continued

	Bearded Seals $n = 30$	Ringed Seals $n = 15$	Ribbon Seals $n = 32$	Spotted Seals $n = 24$
20:3Δ5,11,14	0.06 ± 0.00	0.02 ± 0.01	0.01 ± 0.00	0.03 ± 0.01
22:2NMID	0.06 ± 0.00	0.02 ± 0.01	0.02 ± 0.00	0.03 ± 0.00
22:2Δ7,13	0.13 ± 0.01	0.01 ± 0.01	0.01 ± 0.00	0.01 ± 0.00
22:2Δ7,15	0.31 ± 0.03	0.04 ± 0.04	0.02 ± 0.00	0.02 ± 0.00
Subtotal	0.81 ± 0.04	0.13 ± 0.07	0.09 ± 0.01	0.15 ± 0.01
Total	97.16 ± 0.05	97.53 ± 0.10	97.52 ± 0.04	97.55 ± 0.04
Total n-3	21.10 ± 0.43	28.15 ± 1.39	17.95 ± 0.58	19.57 ± 0.75

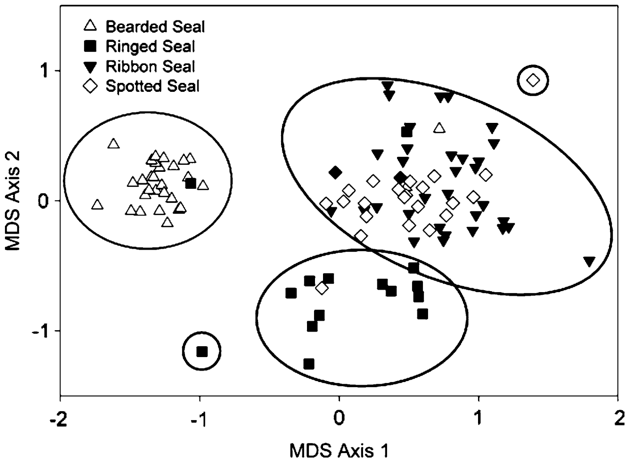

Fig. 1 MDS ordination of blubber FA composition from four species of ice-associated seals (2D Stress of 0.1). Groupings of 90% similarity (*black lines*), based on cluster analysis, are superimposed to verify adequacy of ordination results

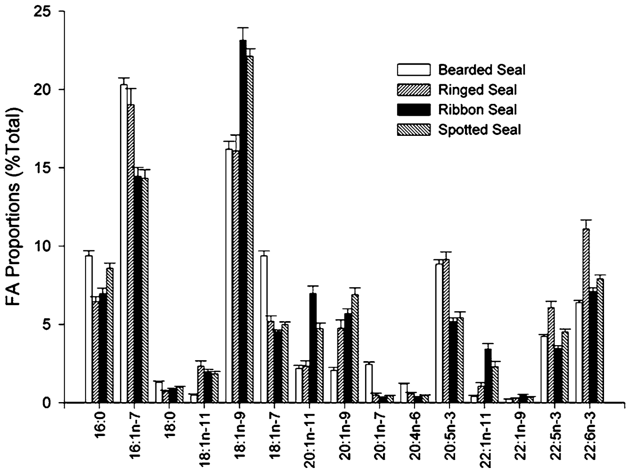

Fig. 2 Proportions of FA (mean ± SE, expressed as mass percent of total FA) primarily responsible for the significant difference (ANOSIM: $R = 0.71$, $P = 0.001$) in blubber FA composition of the four species of ice-associated seals, as indicated by SIMPER analysis

between the concentrations of these FA in bearded and ringed seals were much less marked, but ringed seals did have higher proportions of 18:1n-11, 20:1n-9 and 22:1n-11.

The n-3 FA were extremely important in differentiating the ringed seals from all other species. Ringed seals had a significantly higher proportion of total n-3 FA (28.2 ± 1.4%, $P < 0.001$), with larger amounts of 20:5n-3, 22:5n-3 and 22:6n-3 (Fig. 2; Table 1). In addition, ringed seals had a higher proportion of 16:1n-7, but lower proportions of 18:1n-9, 20:1n-11, 20:1n-9, and 22:1n-11 than the ribbon and spotted seals. Ribbon and spotted seals were the most similar in terms of blubber FA composition, yet ribbon seals tended to have higher concentrations of 20:1n-11 and 22:1n-11.

Discussion

Intraspecific variation

Our data did not indicate any intraspecific differences in FA composition based on sex or age class. We know that the bulk of the samples collected was from juveniles but our data also included adults and pups of both sexes. There seems to be little evidence for differences in FA due to sex in adult bearded (Budge et al. 2007) and ringed seals (Thiemann et al. 2007); studies of foraging behavior and diet of bearded seals (Lowry et al. 1980a; Antonelis et al. 1994; Hjelset et al. 1999), ribbon seals (Deguchi et al. 2004), and ringed seals (Lowry et al. 1980b) also support our conclusion of no difference between sexes.

Differences in FA composition with age class, however, are well known (e.g., Beck et al. 2007; Thiemann et al. 2007). It may be that our data did not show differences between age classes because our samples were not evenly distributed between adults and juveniles. Therefore, our treatment of all samples from a species as a single group may have introduced a degree of variation into our data. Despite this, we were able to detect clear differences in FA compositions between most of these species, suggesting that the intraspecific variation potentially introduced by differences in diets due to age class preferences is far less than the interspecies variation in most cases.

Interspecific and temporal variation

The very high concentrations of n-7 FA in bearded seal blubber were central to differentiating this species from the others and are indicative of a diet rich in benthic molluscs (Joseph 1982). Levels of NMI FA above trace (0.06–0.31%) were another unique feature of bearded seal blubber FA composition. These FA have been identified in a range of benthic invertebrates and appear to be common in bivalves and carnivorous gastropods (Paradis and Ackman 1977; Joseph 1982). In the Bering and Chukchi seas, clams are an important prey item of bearded seals and their utilization appears to be seasonal, occurring primarily in the spring and summer (Burns 1981b). Lowry et al. (1980a) found geographical variation in the utilization of clams as well—although clams constituted a major proportion of the diet in some locations, they represented a very small proportion (~4%) of the diet of bearded seals taken around Little Diomede Island during spring. However, the high concentrations of n-7 and the presence of NMI FA in the bearded seal blubber we analyzed, also sampled on Little Diomede Island in spring, argue for a more typically high contribution of clams to the diet of these animals. The bearded seal blubbers also had a comparatively high concentration of 20:4n-6 relative to the other seal species (Table 1; Fig. 2). Sculpins and shrimp are both particularly rich in 20:4n-6 (Iverson et al. 2002), indicating that these prey are still important in the diet of bearded seals at this location, as they were in the 1970s (Lowry et al. 1980a).

The proportions of major FA in bearded seal blubber reported here are not significantly different from those of bearded seals taken near Little Diomede Island in the spring of 2002 as reported by Budge et al. (2007). However, our results were markedly different from those of West et al. (1979) in that the blubber we analyzed had much lower concentrations of 20:1n-9, 22:1n-11 and the n-3 FA and higher concentrations of 16:1n-7 and 20:4n-6. Because the n-7 fatty acids and 20:4n-6 are common in benthic organisms and 20:1n-9 and 22:1n-11 are more common in pelagic fishes, this difference in FA composition can be interpreted as implying a shift toward a more benthic-dominated diet by bearded seals in the northern Bering Sea since the late 1970s. However, the small sample sizes of West et al. (1979) and the fact that they did not report all isomers of the 16-22 carbon MUFA, nor any NMI FA, make such conclusions tenuous. This comparison also highlights the need to establish consistent methods of blubber sampling and accurate techniques for FA analysis. The data presented here can only serve as a baseline for future work if subsequent studies use similar methods. We followed the methods outlined in Budge et al. (2006) for sampling and FA analyses that employed a polar capillary column and allowed identification of ~70 FA. For other groups working in this field, we recommend similar methods with careful validation of FA results.

Comparison of our data with the blubber FA composition of bearded seals from more recent studies in northeastern Canada (Durnford and Shahidi 2002) and the area surrounding Svalbard, Norway (Grahl-Nielsen et al. 2003) reveals regional differences. The most pronounced difference is the lower concentration of 20:1n-9 and 22:1n-11 in seals from the northern Bering Sea. Our animals also had generally lower concentrations of the n-3 FA, particularly 22:6n-3. Both observations imply a more benthic-dominated diet in bearded seals of the northern Bering Sea. Unfortunately, neither of the above studies reported NMI FA concentrations, which would have been helpful in assessing the validity of this conclusion. The blubber FA composition of ringed seals from the northern Bering Sea was remarkably similar to that reported for other arctic regions (Durnford and Shahidi 2002; Grahl-Nielsen et al. 2003, 2005).

Although arctic cod is believed to make up the majority of the ringed seals' diet in winter, stomach content analysis from ringed seals sampled near Little Diomede Island in spring in the 1970s indicated that their main prey were benthic invertebrates, with shrimp constituting 44% of the diet, gammarid amphipods making up 15% and arctic cod making up the bulk of the remainder of the diet (Lowry et al. 1980b). Shrimps are high in 20:5n-3 and 22:6n-3 but relatively low in 20:1n-9 and 22:1n-11 (Iverson et al. 2002). Thus, our data showing a similar pattern of high concentrations of n-3 FA and lower concentrations of 20:1n-9 and 22:1n-11 in their blubber support the conclusion that shrimp are still an important prey item for ringed seals in spring.

It is not surprising that ribbon and spotted seals could not be differentiated by their FA compositions (Fig. 1) as they occupy similar habitats (Simpkins et al. 2003) and arctic cod is thought to be the primary prey item for both species in the northern Bering Sea during spring (Frost and Lowry 1980; Bukhtiyarov et al. 1984; Lowry et al. 2000). Additionally, adult ribbon and spotted seals sampled near Little Diomede Island in summer had similar nitrogen isotope ratios (Dehn et al. 2007), further supporting a similarity in diet.

Blubber samples from both ribbon and spotted seals had particularly high concentrations of 20:1n-11, 20:1n-9 and 22:1n-11 compared to bearded and ringed seals (Table 1; Fig. 2). Although vertebrates can theoretically synthesize 20:1n-9 and 22:1n-11, these FA primarily originate from the fatty alcohols in wax esters of calanoid copepods (Lee et al. 1971; Pascal and Ackman 1976; Ackman et al. 1980; Falk-Petersen et al. 1990). 20:1n-11 is typically found only in higher trophic level predators and is the product of the partial chain-shortening of 22:1n-11 (Norseth and Christophersen 1978; Bremer and Norum 1982; Cooper et al. 2006). The concentrations of 20:1n-9 and 22:1n-11 vary widely among different fish and invertebrate species (Graeve et al. 1997; Budge et al. 2002; Iverson et al. 2002), making them good indicators of diet when found in a predator.

Ribbon and spotted seals feed primarily on Arctic cod but have also been shown to include other fish such as pollock, herring and capelin in their diet (Frost and Lowry 1980; Bukhtiyarov et al. 1984; Dehn et al. 2007). Planktivorous fish tend to have high levels of these copepod-derived FA (Graeve et al. 1997; Budge et al. 2002; Iverson et al. 2002), thus explaining the high concentrations found in ribbon and spotted seals. Despite broad similarities in the FA compositions of the two species, ribbon seals had a higher concentration of 22:1n-11 than spotted seals and the reverse was true for 20:1n-9 (Table 1). The ratio of 20:1n-9 to 22:1n-11 is greater than one in Arctic cod (Falk-Petersen et al. 2004) but less than one in pollock, herring and capelin (Budge et al. 2002; Iverson et al. 2002). This may indicate that spotted seals we sampled relied more heavily on Arctic cod than did the ribbon seals. Spotted seals were found to consume octopus in spring (Lowry et al. 2000) and octopus have a 20:1n-9 to 22:1n-11 ratio greater than one (Iverson et al. 2002), so consumption of octopus may have also contributed to the higher concentration of 20:1n-9 in spotted seals relative to ribbon seals.

Vulnerability to ecosystem changes

With our current data set, we are attempting to establish baseline FA information for diet estimates to help explain potential future variation in marine mammal populations and in food web productivity of the northern Bering Sea. Changes in marine mammal populations in response to regional fluctuations in climate have been documented in several ecosystems, but without the corresponding FA data to assist with diet interpretation. For example, in the southern Indian Ocean, temperatures increased from the 1960s to 1980s and following a time lag, populations of the majority of top predators (both seabirds and seals) decreased dramatically (Weimerskirch et al. 2003). Exceptions include King Penguins and Amsterdam fur seals, whose populations increased over the same time period. Both of these predators prey primarily on myctophid fishes, whereas the species that declined are primarily squid eaters, and to a lesser degree crustacean and fish predators. In another case, the sympatric Galapagos fur seals (*Arctocephalus galapagoensis*) and Galapagos sea lions (*Zalophus californianus*) exhibited 50–70 and 30% declines, respectively, in response to the 1982–1983 El Nino event (Trillmich and Limberger 1985). Otariids generally appear to be opportunistic feeders (Antonelis et al. 1984; Green et al. 1991; Gales and Pemberton 1994), which may buffer them against environmental changes, but the barrier to emigration and the narrowly defined ecosystem created by the isolation of the Galapagos Islands likely makes the Galapagos fur seals and sea lions particularly vulnerable to environmental fluctuations. With both of these studies, FA data would have helped clarify the role of dietary shifts in the change in abundance of those populations.

In the northern Bering Sea, the reduction in sea ice and increase in air and ocean temperatures has coincided with a reduction in some benthic prey populations and an increase in some benthic and pelagic fishes, constituting a northward shift of pelagic taxa characteristic of the southeastern Bering Sea (Overland and Stabeno 2004; Grebmeier et al. 2006; Mueter and Litzow 2008). Bluhm and Gradinger (2008) predicted that in the future a shift to a more pelagic food web-dominated ecosystem will be common and occur over a geographically large area within the Arctic. Bearded seals are generally believed to rely more heavily on benthic prey than ringed, ribbon and spotted seals (Lowry et al. 1980a; Burns 1981a; Antonelis et al. 1994; Dehn et al. 2007), which is supported by our data. In light of the observed and predicted shift to pelagic food web-dominated ecosystems, bearded seals may be particularly vulnerable. Still, despite a greater reliance on benthic prey, bearded seals are feeding generalists and Laidre et al. (2008) believe that they will likely be able to make the switch from benthic dominated to pelagic dominated diets if there are disruptions in the benthic environment.

Close comparison of our 2003 FA data for bearded seals to those from animals collected in May–June 2002 at Little Diomede Island (Budge et al. 2007) reveals some significant differences. Overall, the major FA in bearded seal blubber are quite similar between the 2 years, as described above; however, in 2003 the minor NMID FA, associated with a variety of benthic invertebrates, shifted to resemble levels found in the Pacific walrus (*Odobenus rosmarus*; Fig. 3; ANOSIM: $R = 0.19$, $P < 0.001$). This may simply reflect normal interannual variation in diet, or it may represent the beginning of a shift in diet to one more similar to that of the walrus. If the latter can be shown to be true through analysis of more recent blubber samples, it might argue against the purported significance of changes in benthic production in the northern Bering Sea in recent years, and perhaps indicate greater competition with walrus for common prey resources.

Laidre et al. (2008) quantified the sensitivity of Arctic and sub-Arctic marine mammals to long-term unidirectional climate warming based on various factors including: population size, breadth/extent of geographic range, habitat specificity, diet diversity, migrations, individual site fidelity, influences of changes in sea ice, influences of changes in trophic web and maximum rate of population increase. Obviously, monitoring diet with blubber FA will only provide a small portion of the information necessary to explain variation in seal populations due to climate change. However, in some situations, blubber FA may be important in demonstrating that an observed change in behavior has little to do with variation in prey availability. For instance, ringed seals are one of the few species where climate-related declines in abundance and changes in demography have already been documented. The declines in reproduction and juvenile survival seen in the southeastern Beaufort sea in the mid 1970s and 1980s were due to severe ice conditions (Stirling 2002), and pups in subnivean lairs are also

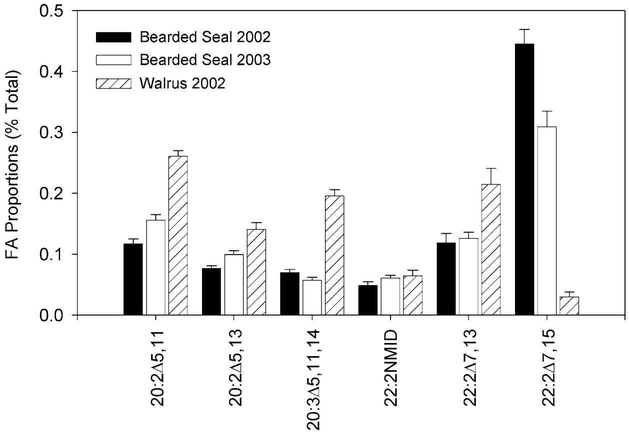

Fig. 3 Proportions of NMID FA (mean ± SE, expressed as mass percent of total FA) in bearded seal and walrus blubber collected in 2002 (from Budge et al. 2007) and in bearded seal blubber collected in 2003 at Little Diomede Island. The bearded seal blubber NMID FA composition is significantly different in the 2 years (ANOSIM: $R = 0.19$, $P < 0.001$)

vulnerable to warm weather and excessive rain during the pupping period (Stirling and Smith 2004). Thus, this species may be particularly sensitive to changes in their sea ice habitat, with less influence from changing prey availability. In this situation, we would expect blubber FA data to show little change in diet, eliminating prey availability as a factor.

Similarly, Laidre et al. (2008) suggested that ribbon and spotted seals are more sensitive to Arctic warming, due to limited geographic distribution, site fidelity and migration. While these factors may contribute to the vulnerability of these species, spotted and ribbon seals may be able to make northward extensions of their range as was seen for the harp seals (*Phoca groenlandica*) and harbor seals (*P. vitulina*) in West Greenland and western Hudson Bay, respectively, during periods of warmer temperatures and light sea ice (Laidre et al. 2008 and references therein). Corresponding to the northward range extension of harp and harbor seals, ringed seals in both areas exhibited a northward retraction of their ranges. Whether this was due to competition from the harp and harbor seals or to a shift in availability of preferred prey is not known. Interspecific competition among the ice seals resident in the Bering Sea may, therefore, become stronger in response to warming trends. This potential issue of competition lends itself particularly well to examination with FA data; the data presented here will be invaluable in interpreting future results.

Studying diet composition over time is one way to monitor the response of a species to ecosystem changes. In addition, because arctic pinnipeds may act as indicators of the regional effects of climate change (Tynan and DeMaster 1997; Laidre et al. 2008), documenting variability in diets of these predators will be important to our understanding of not only their populations, but also the broader Arctic environment. We believe that blubber FA analysis will be a useful tool in assessing the response of these species and ecosystems to changes associated with arctic warming and climate change.

Acknowledgments We thank the residents of Little Diomede Island for providing samples from the subsistence hunts during spring 2003. Seal specimen collections were authorized by National Marine Fisheries Service Scientific Research Permit No. 358-1585. Funding for this project was provided by the Cooperative Institute for Arctic Research. Additional support came from the National Science Foundation (Grant # OPP 9910319) and the Natural Sciences and Engineering Research Council (NSERC) of Canada. Thanks also to SJ Iverson for generously supporting a portion of the experimental analysis.

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