Variation in blubber fatty acid composition among marine mammals in the Canadian Arctic

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ABSTRACT

The composition of predator adipose stores can provide important insights into foraging patterns and the ecological relationships among species. We determined the fatty acid (FA) composition of 843 blubber samples from 80 bearded seals (*Erignathus barbatus*), 33 harbor seals (*Phoca vitulina*), 239 harp seals (*Pagophilus groenlandicus*), 32 hooded seals (*Cystophora cristata*), 281 ringed seals (*Phoca hispida*), 53 walruses (*Odobenus rosmarus rosmarus*), 105 beluga whales (*Delphinapterus leucas*), and 20 narwhals (*Monodon monoceros*) across the Canadian Arctic to examine patterns of variability among and within species. FA signatures accurately distinguished phocid seals, walruses, and whales. Belugas and narwhals had the most similar FA signatures of any two species, suggesting substantial overlap in their diets, especially in the narwhal-wintering area off eastern Baffin Island. Among phocid seals, harp and hooded seals had the most similar FA signatures. Bearded seals were most similar to walruses, which was consistent with the benthic feeding habits of both species. Within species, geographic differences in FA signatures were found over both large (>4,000 km) and small (<100 km) spatial scales. Overall, within-species differences were smaller than among-species differences. In general, FA signature patterns were consistent with previous studies of the ecology and diets of arctic marine mammals.

Key words: arctic, marine mammal, blubber, fatty acid, foraging, diet, Pinnipedia, Cetacea.

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Accurate information on the foraging ecology of predators is essential to the understanding of marine ecosystems. In the Canadian Arctic, long-term environmental changes appear to be having significant impacts on the habitat (Johannessen *et al.* 1999, Gough *et al.* 2004, Johnston *et al.* 2005, Comiso 2006), body condition (Stirling *et al.* 1999, Stirling and Parkinson 2006), recruitment (Stirling and Smith 2004, Ferguson *et al.* 2005, Stirling 2005), and abundance (Tynan and DeMaster 1997, Regehr *et al.*, in press) of marine mammals. Climate warming has had large-scale effects on arctic food webs, resulting in apparent changes in fish populations and subsequent shifts in the diets of avian predators (Gaston *et al.* 2003). Preliminary evidence also suggests that recent changes in prey distributions have caused shifts in the diets of polar bears (*Ursus maritimus*, Iverson *et al.* 2006). Baseline information on how marine mammal diets vary across and within species is therefore essential to effectively monitoring future shifts in marine ecosystems and developing a predictive capability about how various populations may respond to environmental change.

The analysis of predator fatty acid (FA) stores can provide important insights into foraging patterns over multiple temporal and spatial scales (*e.g.*, Iverson *et al.* 1997, 2004; Dahl *et al.* 2000; Bradshaw *et al.* 2003; Beck *et al.* 2005, 2007). Because vertebrate carnivores have a limited ability to synthesize and modify FA, many dietary FA are directly or predictably incorporated into their adipose tissue (*e.g.*, Ackman and Eaton 1966; Brockerhoff *et al.* 1967; Rouvinen and Kiiskinen 1989; Iverson *et al.* 1995, 2004; Dalsgaard and St. John 2004; Käkelä *et al.* 2006). As a result, the composition of adipose stores will reflect the integrated composition of the diet over a span of weeks to months (Kirsch *et al.* 2000, Iverson *et al.* 2004). The development of FA analysis as an ecological tool has reached the point where the relative abundance of multiple FA in a predator (*i.e.*, the FA signature) can be used to produce a quantitative estimate of predator diet composition (see Iverson *et al.* 2004). However, such quantitative analyses require, among other things, an extensive database on the FA composition of all potential prey species. In the absence of these data, predator FA signatures alone can provide information on regional and demographic foraging patterns (*e.g.*, Smith *et al.* 1996, Iverson *et al.* 1997, Raclot *et al.* 1998, Falk-Petersen *et al.* 2004, Beck *et al.* 2005, Thiemann *et al.* 2007*a*). Because all mammalian carnivores have similar limitations on FA synthesis and modification, among-species differences in FA signatures are primarily attributable to differences and patterns in foraging and can provide information on trophic relationships among predator species.

To date, most information on the diets and foraging habits of arctic marine mammals has come from analyses of stomach contents (*e.g.*, Finley and Gibb 1982, Finley and Evans 1983, Finley *et al.* 1990, Fisher and Stewart 1997, Holst *et al.* 2001). Because these data are based on the recovery of prey structures consumed in a recent meal, the contribution of soft-bodied, readily digestible prey is usually underestimated, and longer-term dietary patterns are not reflected. Furthermore, the use of different methods for quantifying stomach contents (*e.g.*, percent frequency, percent volume, relative energy intake) makes it difficult to detect trends among species, across regions, or over time. Aside from the identification of some common prey species, relatively little is known about the overall dietary similarity of several species of arctic marine mammals. For instance, although bearded seals (*Erignathus barbatus*) and walruses (*Odobenus rosmarus*) likely feed at lower trophic levels than other arctic pinnipeds (see Lowry *et al.* 1980*a*, Pauly *et al.* 1998), distinctions between these two species and among other seals and whales have been less obvious (see Lowry *et al.* 1980*a*, Hobson and Welch 1992, Pauly *et al.* 1998). Using stable isotope analysis, Hobson and Welch (1992) concluded that belugas (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*)

in the High Arctic occupied trophic levels of 3.9 and 3.7 out of 5, respectively, which is intermediate between walruses at 2.9 and ringed seals (*Phoca hispida*) and bearded seals at 4.1 and 4.0, respectively. In contrast, Pauly *et al.* (1998) reviewed data from across the Arctic and assigned walruses and bearded seals identical trophic levels of 3.4, and harp seals (*Pagophilus groenlandicus*), hooded seals (*Cystophora cristata*), harbor seals (*Phoca vitulina*), ringed seals, beluga whales, and narwhals all ranged from 4.0 to 4.2. To a large degree, the different findings of these two large-scale studies likely reflect regional differences in foraging patterns, but the variation also illustrates the need for greater resolution of trophic relationships across arctic marine ecosystems.

We analyzed the blubber FA composition of bearded seals, harbor seals, harp seals, hooded seals, ringed seals, walruses, beluga whales, and narwhals across the Canadian Arctic. We used these data to make inferences about the dietary relationships among species and to examine the geographic variability in FA signatures within species over multiple spatial scales. In addition to providing insights into the structure of arctic food webs, this study aimed to establish baseline data that could aid in the detection of future shifts in arctic ecosystems as well as provide a foundation for future analyses of the diets of polar bears, which feed on these same species of marine mammals (*e.g.*, Iverson *et al.* 2006).

METHODS

Sample Collection

From 1992 to 2004, blubber samples were collected from 843 marine mammals across the Canadian Arctic (Fig. 1, Table 1). Samples were collected from animals of every age class harvested by native subsistence hunters or sampled during the course of other marine mammal research projects. The specific locations from which samples were collected were determined solely by availability. Large tissue samples (approximately 10–60 cm^2) extending through the depth of the blubber layer and including a portion of attached muscle were wrapped in foil and stored frozen until analysis. In the lab, a biopsy subsample was taken through the full depth of the adipose layer in the center of each sample, an area that is protected from oxidation during frozen storage (Budge *et al.* 2006).

Lipid and Statistical Analyses

Lipid was extracted and isolated from each biopsy subsample according to Iverson *et al.* (2001). FA methyl esters (FAME) were prepared from each extracted lipid sample using H_2SO_4 as a catalyst (Thiemann *et al.* 2004, Budge *et al.* 2006), and duplicate analyses and identification of FAME were performed using temperature-programmed gas-liquid chromatography according to Iverson *et al.* (1997, 2002) and Budge *et al.* (2002, 2006). Approximately sixty-five FA were routinely identified in most blubber samples and expressed as the mass percent of total FA $\pm$ SEM. FA are referred to by the standard nomenclature of carbon chain length:number of double bonds, and location (n-x) of the double bond nearest the terminal methyl group (IUPAC-IUB 1967).

A combination of hierarchical cluster analysis, multivariate analysis of variance (MANOVA), and discriminant analysis (SPSS 1997, Budge *et al.* 2006) was used to examine variability in marine mammal FA signatures by species and location.
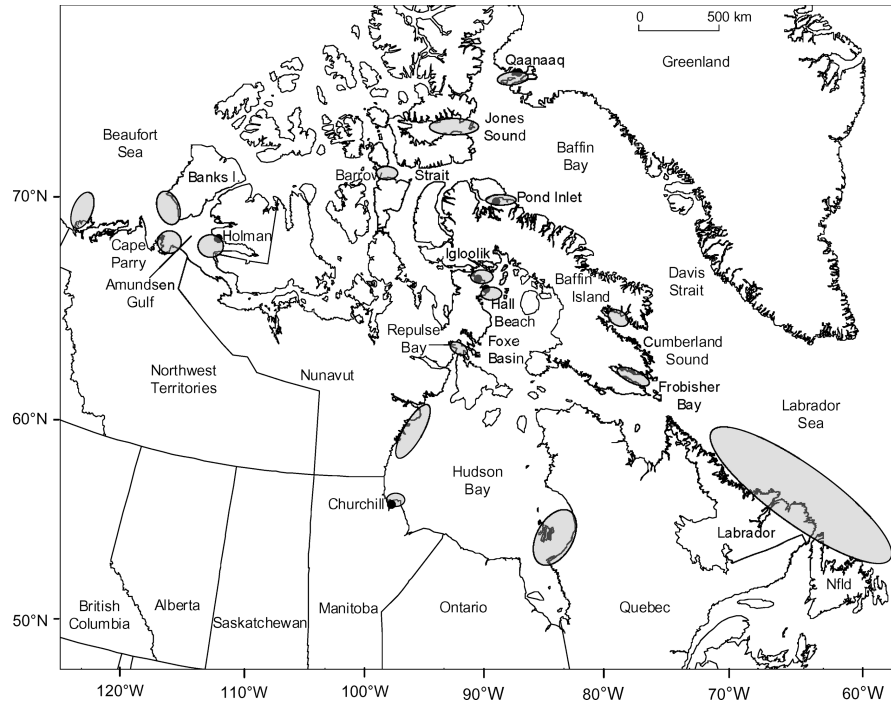
Figure 1. Locations of marine mammals sampled across the Canadian Arctic. Species distributions and sample sizes are listed in Table 1.

Because hierarchical cluster analysis compares average signatures, all sixty-five FA could be used despite small sample sizes for some groups. However, for MANOVA and discriminant analyses, the n of any group must exceed the number of response variables (Stevens 1986, Legendre and Legendre 1998). Thus, the values of the seventeen most abundant and/or most variable FA were transformed by calculating the log of the ratio of each FA to 18:0 to improve normality for these analyses (see Budge *et al*. 2002, 2006; Iverson *et al*. 2002). These seventeen FA included those that were abundant in marine mammal blubber as well as those that serve as important dietary indicators (see Iverson *et al*. 2004). Smaller subsets of FA (minimum of eleven) were used in some analyses following the constraints of smaller group sizes.

Among species, original and cross-validated classification rates were used to assess the ability of discriminant analyses to distinguish species by their FA signatures. Cross-validation was performed by classifying each individual animal against the functions derived from all other animals. Within species, regional variability in the FA signatures of bearded seals, harbor seals, walruses, and beluga whales was tested by MANOVA. Because they were sampled in several different locations, bearded seals and belugas were also examined by discriminant analysis after pooling individuals into larger geographic groups. Harp and hooded seals were sampled in a single location each, and too few narwhals were sampled to rigorously examine spatial patterns. Regional differences in ringed seal FA were examined previously (Thiemann *et al*. 2007*a*).

Table 1. Number of marine mammals sampled in nine regions across the Canadian Arctic. Locations are plotted in Figure 1.

Species	Total n	Location	Samples
Bearded seal	80	Frobisher Bay	7
		Newfoundland and Labrador	40
		Jones Sound	1
		Holman	14
		Banks Island	2
		Cape Parry	4
		NW Hudson Bay	12
Harbor seal	33	Churchill River	18
		NW Hudson Bay	15
Harp seal	239	Newfoundland and Labrador	239
Hooded seal	32	Newfoundland and Labrador	32
Ringed seal	281	Frobisher Bay	27
		Newfoundland and Labrador	29
		Qaanaaq	42
		Jones Sound	41
		Holman	43
		Banks Island	39
		Cape Parry	7
		SE Hudson Bay	23
		NW Hudson Bay	30
Walrus	53	Hall Beach	25
		Igloolik	28
Beluga whale	105	Cumberland Sound	4
		Frobisher Bay	10
		Igloolik	26
		Jones Sound	5
		Barrow Strait	3
		Holman	9
		Western NWT	20
		SE Hudson Bay	16
		NW Hudson Bay	12
Narwhal	20	Pond Inlet	3
		Repulse Bay	7
		Jones Sound	10
Total	843		843

Because of the opportunistic nature of sample collection, we did not have sufficient samples or data to rigorously test demographic, interannual, or seasonal differences within species. However, most species were sampled within a limited seasonal time frame. For instance, all harp and hooded seals were sampled in late winter and early spring. Belugas, narwhals, and walruses were sampled in the summer whereas harbor seals were sampled in the fall and winter. Samples were collected in several different seasons only from bearded and ringed seals. For bearded seals, insufficient samples were available from any one region to test for seasonal differences. For ringed seals, Thiemann *et al.* (2007*a*) found evidence of seasonal variability in juvenile FA signatures off the coast of Labrador (the only area where samples were collected in more than one season). Although we could not exclude the possible confounding

influences of season or year in this study, Thiemann *et al.* (2007*a*) concluded that regional differences in ringed seal FA signatures generally exceed demographic and temporal variability.

RESULTS

Species Differences in Blubber FA Composition

The blubber FA composition of marine mammals differed significantly across species (Table 2; MANOVA: Wilks' $\lambda < 0.001$, $P < 0.001$), with differences occurring in all seventeen FA examined. Overall, discriminant analysis (Fig. 2) classified 94.4% of original samples and 93.2% of cross-validated samples to their correct species. The most common misclassification occurred between beluga whales and narwhals; 8.6% of cross-validated beluga samples were misclassified as narwhals, whereas 20% of cross-validated narwhals were misclassified as belugas. Bearded seals and hooded seals were identified with 92.5% and 90.6% accuracy, respectively. Ringed seal samples were correctly classified 95.4% of the time, with 2.1% of cross-validated samples misclassified as harp seals. Harp seal samples were identified with 92.9% accuracy, with 2.5% of cross-validated samples being misclassified as ringed seals. Harbor seals and walruses were correctly classified 100% of the time.

Hierarchical cluster analysis of average FA signatures initially separated walruses from all other species and then separated whales from phocid seals (Fig. 3). Among all eight species, beluga whales and narwhals had the most similar FA signatures, although they still differed in six of the seventeen FA examined in MANOVA. Among phocid seals, harp and hooded seals were most similar, although bearded seals across the Canadian Arctic and harbor seals in western Hudson Bay also grouped closely. Cluster analysis of species pooled across all regions indicated that ringed seals may have the most distinctive FA signature of all arctic phocids. However, these groupings did not incorporate regional variability and may have been influenced by uneven sample sizes across species.

Geographic Differences in Blubber FA Composition

To compare the relative effects of species and location on the FA signatures of arctic marine mammals, we performed hierarchical cluster analysis on species data grouped by location (Fig. 4). Because of small sample sizes, animals from some areas were combined into larger groups. To the extent that sample sizes would allow, our objective was to obtain the finest spatial resolution possible. Major clusters in the analysis were formed by whales, harbor seals, ringed seals, and the two benthic foragers, walruses and bearded seals. Similar to the cluster analysis of species averages (Fig. 3), whales and seals were generally separated in the first split, with beluga whales and narwhals appearing to have similar FA profiles. However, in contrast to Figure 3, harp and hooded seals from Newfoundland and Labrador clustered with belugas from Frobisher Bay, and walruses clustered with bearded seals. The third split in the analysis separated harbor seals from ringed seals, bearded seals, and walruses. Overall, groups from different areas tended to cluster together by species.

Among bearded seals, samples from two eastern Arctic locations—Frobisher Bay and the coast of Labrador—had the most similar FA signatures whereas those from

Table 2. Fatty acid composition and major lipid classes (mass % of total FA ± SEM) of blubber samples collected from marine mammals across the Canadian Arctic. Although sixty-five FA were routinely identified and quantified, only the fifty-one FA that averaged >0.1% across all species are listed.

Species: N:	Bearded seal 80	Harbor seal 33	Harp seal 239	Hooded seal 32	Ringed seal 281	Atlantic walrus 53	Beluga 105	Narwhal 20
SAT								
12:0	0.15 ± 0.01	0.13 ± 0.00	0.09 ± 0.00	0.09 ± 0.01	0.10 ± 0.00	0.10 ± 0.01	0.91 ± 0.04	0.86 ± 0.06
14:0*	3.15 ± 0.06	2.81 ± 0.09	5.20 ± 0.06	5.15 ± 0.12	3.75 ± 0.06	3.04 ± 0.07	5.72 ± 0.09	5.17 ± 0.16
Iso15	0.13 ± 0.00	0.19 ± 0.01	0.17 ± 0.00	0.17 ± 0.01	0.15 ± 0.00	0.07 ± 0.00	0.84 ± 0.07	0.89 ± 0.07
Anti15	0.19 ± 0.02	0.12 ± 0.01	0.07 ± 0.00	0.07 ± 0.00	0.08 ± 0.00	0.74 ± 0.06	0.13 ± 0.01	0.15 ± 0.01
15:0	0.35 ± 0.01	0.24 ± 0.01	0.25 ± 0.00	0.29 ± 0.01	0.20 ± 0.00	0.40 ± 0.01	0.30 ± 0.01	0.27 ± 0.01
Iso16	0.17 ± 0.01	0.13 ± 0.01	0.07 ± 0.00	0.08 ± 0.00	0.07 ± 0.00	0.13 ± 0.00	0.31 ± 0.03	0.39 ± 0.03
16:0*	9.41 ± 0.17	8.63 ± 0.31	8.27 ± 0.10	10.13 ± 0.32	5.66 ± 0.12	10.07 ± 0.30	6.76 ± 0.12	6.88 ± 0.39
7Me16:0	0.29 ± 0.01	0.29 ± 0.01	0.27 ± 0.00	0.26 ± 0.01	0.30 ± 0.00	0.26 ± 0.01	0.30 ± 0.01	0.26 ± 0.01
Iso17	0.32 ± 0.01	0.27 ± 0.02	0.10 ± 0.00	0.12 ± 0.00	0.10 ± 0.00	0.62 ± 0.02	0.20 ± 0.01	0.18 ± 0.01
17:0	0.25 ± 0.01	0.15 ± 0.01	0.11 ± 0.01	0.16 ± 0.01	0.07 ± 0.00	0.28 ± 0.01	0.10 ± 0.01	0.08 ± 0.00
18:0	1.67 ± 0.05	1.05 ± 0.04	1.24 ± 0.03	1.66 ± 0.07	0.63 ± 0.01	2.15 ± 0.10	0.96 ± 0.04	0.84 ± 0.07
MUFA								
14:1n-9	0.12 ± 0.01	0.11 ± 0.01	0.18 ± 0.00	0.13 ± 0.01	0.18 ± 0.00	0.16 ± 0.01	0.82 ± 0.04	0.75 ± 0.08
14:1n-7	0.08 ± 0.00	0.14 ± 0.01	0.04 ± 0.00	0.04 ± 0.00	0.09 ± 0.00	0.09 ± 0.00	0.68 ± 0.04	0.73 ± 0.07
14:1n-5	0.60 ± 0.03	1.15 ± 0.06	0.49 ± 0.02	0.48 ± 0.06	1.24 ± 0.03	0.50 ± 0.05	1.90 ± 0.09	1.89 ± 0.13
16:1n-11	0.33 ± 0.01	0.33 ± 0.01	0.38 ± 0.01	0.44 ± 0.01	0.57 ± 0.01	0.30 ± 0.01	1.18 ± 0.05	1.16 ± 0.24
16:1n-9	0.34 ± 0.01	0.66 ± 0.02	0.25 ± 0.01	0.30 ± 0.01	0.49 ± 0.01	0.37 ± 0.01	1.39 ± 0.06	1.71 ± 0.14
16:1n-7*	19.10 ± 0.45	19.11 ± 0.51	12.88 ± 0.21	11.36 ± 0.50	18.97 ± 0.19	17.88 ± 0.59	22.61 ± 0.48	23.03 ± 0.69
17:1	0.37 ± 0.01	0.48 ± 0.02	0.19 ± 0.01	0.25 ± 0.02	0.20 ± 0.01	0.32 ± 0.01	0.21 ± 0.01	0.13 ± 0.03
18:1n-13	0.30 ± 0.01	0.21 ± 0.02	0.17 ± 0.07	0.09 ± 0.00	0.09 ± 0.00	0.57 ± 0.02	0.07 ± 0.00	0.04 ± 0.01
18:1n-11	1.04 ± 0.08	0.71 ± 0.09	2.40 ± 0.06	2.21 ± 0.11	3.37 ± 0.11	0.13 ± 0.01	3.81 ± 0.08	5.42 ± 0.18
18:1n-9*	14.02 ± 0.27	21.44 ± 0.74	11.25 ± 0.22	16.39 ± 0.70	13.34 ± 0.18	14.17 ± 0.36	14.99 ± 0.22	18.31 ± 0.45
18:1n-7*	8.08 ± 0.17	6.19 ± 0.16	3.43 ± 0.07	3.41 ± 0.16	4.24 ± 0.06	10.81 ± 0.23	3.71 ± 0.06	3.25 ± 0.11
18:1n-5	0.55 ± 0.01	0.55 ± 0.02	0.54 ± 0.01	0.47 ± 0.01	0.55 ± 0.01	0.42 ± 0.02	0.48 ± 0.01	0.42 ± 0.02
20:1n-11*	1.13 ± 0.04	0.46 ± 0.04	1.60 ± 0.05	1.54 ± 0.08	1.48 ± 0.05	1.15 ± 0.05	2.78 ± 0.10	4.04 ± 0.15
20:1n-9*	3.89 ± 0.24	2.51 ± 0.19	12.48 ± 0.29	11.51 ± 0.53	7.60 ± 0.20	1.82 ± 0.07	8.13 ± 0.25	8.07 ± 0.39
20:1n-7	1.49 ± 0.05	0.49 ± 0.02	0.85 ± 0.04	0.62 ± 0.05	0.64 ± 0.02	4.22 ± 0.17	0.62 ± 0.02	0.57 ± 0.04

Continued.

Table 2. Continued

Species: N:	Bearded seal 80	Harbor seal 33	Harp seal 239	Hooded seal 32	Ringed seal 281	Atlantic walrus 53	Beluga 105	Narwhal 20
22:1n-11*	0.98 ± 0.12	0.32 ± 0.04	7.00 ± 0.24	5.97 ± 0.41	1.75 ± 0.09	0.10 ± 0.01	4.15 ± 0.21	4.12 ± 0.41
22:1n-9*	0.31 ± 0.02	0.14 ± 0.01	1.13 ± 0.04	0.94 ± 0.06	0.53 ± 0.02	0.11 ± 0.01	0.81 ± 0.05	0.71 ± 0.08
22:1n-7	0.10 ± 0.01	0.02 ± 0.00	0.17 ± 0.01	0.11 ± 0.01	0.08 ± 0.00	0.13 ± 0.01	0.14 ± 0.01	0.10 ± 0.01
24:1n-9	0.08 ± 0.01	0.06 ± 0.01	0.21 ± 0.01	0.20 ± 0.01	0.06 ± 0.00	0.06 ± 0.00	0.12 ± 0.01	0.12 ± 0.01
PUFA								
16:2n-4	0.20 ± 0.01	0.39 ± 0.02	0.19 ± 0.01	0.24 ± 0.01	0.15 ± 0.01	0.07 ± 0.00	0.22 ± 0.01	0.12 ± 0.02
16:3n-6	0.39 ± 0.01	0.23 ± 0.01	0.57 ± 0.01	0.36 ± 0.02	0.65 ± 0.01	0.36 ± 0.01	0.57 ± 0.01	0.46 ± 0.02
16:3n-4	0.18 ± 0.01	0.10 ± 0.01	0.34 ± 0.01	0.19 ± 0.02	0.30 ± 0.01	0.11 ± 0.01	0.15 ± 0.01	0.16 ± 0.02
16:4n-1	0.23 ± 0.02	0.08 ± 0.01	0.58 ± 0.02	0.33 ± 0.03	0.43 ± 0.02	0.22 ± 0.01	0.13 ± 0.01	0.09 ± 0.01
18:2n-6*	1.65 ± 0.07	2.03 ± 0.07	1.21 ± 0.02	1.39 ± 0.03	1.19 ± 0.03	0.67 ± 0.02	1.21 ± 0.04	1.04 ± 0.08
18:2n-4	0.19 ± 0.00	0.10 ± 0.00	0.10 ± 0.00	0.09 ± 0.00	0.12 ± 0.00	0.36 ± 0.01	0.08 ± 0.00	0.04 ± 0.01
18:3n-6	0.18 ± 0.01	0.14 ± 0.01	0.11 ± 0.00	0.11 ± 0.00	0.16 ± 0.00	0.14 ± 0.00	0.09 ± 0.00	0.10 ± 0.01
18:3n-4	0.14 ± 0.01	0.10 ± 0.01	0.12 ± 0.00	0.07 ± 0.01	0.08 ± 0.00	0.25 ± 0.02	0.09 ± 0.00	0.07 ± 0.01
18:3n-3*	0.33 ± 0.01	0.88 ± 0.05	0.51 ± 0.02	0.56 ± 0.03	0.42 ± 0.01	0.20 ± 0.01	0.26 ± 0.01	0.25 ± 0.01
18:4n-3*	0.77 ± 0.03	1.05 ± 0.08	1.49 ± 0.04	1.50 ± 0.11	1.06 ± 0.03	0.70 ± 0.03	0.39 ± 0.02	0.23 ± 0.02
18:4n-1	0.16 ± 0.01	0.05 ± 0.01	0.21 ± 0.01	0.14 ± 0.01	0.15 ± 0.00	0.32 ± 0.01	0.12 ± 0.00	0.11 ± 0.01
20:2n-6	0.49 ± 0.02	0.35 ± 0.01	0.20 ± 0.00	0.28 ± 0.01	0.20 ± 0.00	0.58 ± 0.02	0.15 ± 0.01	0.15 ± 0.01
20:3n-6	0.13 ± 0.01	0.11 ± 0.01	0.06 ± 0.00	0.12 ± 0.01	0.09 ± 0.00	0.23 ± 0.01	0.06 ± 0.00	0.06 ± 0.00
20:4n-6	1.03 ± 0.03	1.04 ± 0.05	0.30 ± 0.01	0.30 ± 0.01	0.37 ± 0.01	0.55 ± 0.01	0.25 ± 0.01	0.17 ± 0.01
20:4n-3*	0.47 ± 0.01	0.62 ± 0.04	0.54 ± 0.01	0.75 ± 0.04	0.38 ± 0.01	0.69 ± 0.02	0.34 ± 0.01	0.21 ± 0.02
20:5n-3*	8.91 ± 0.20	5.78 ± 0.32	7.08 ± 0.12	5.91 ± 0.33	9.43 ± 0.13	8.21 ± 0.37	3.37 ± 0.11	2.06 ± 0.20
21:5n-3	0.46 ± 0.01	0.27 ± 0.01	0.41 ± 0.00	0.38 ± 0.01	0.40 ± 0.00	0.83 ± 0.02	0.14 ± 0.01	0.08 ± 0.01
22:4n-6	0.26 ± 0.01	0.40 ± 0.04	0.06 ± 0.00	0.03 ± 0.00	0.07 ± 0.00	0.34 ± 0.02	0.04 ± 0.00	0.02 ± 0.00
22:5n-6	0.18 ± 0.01	0.23 ± 0.02	0.09 ± 0.00	0.09 ± 0.01	0.09 ± 0.00	0.09 ± 0.00	0.06 ± 0.00	0.02 ± 0.00
22:5n-3*	4.56 ± 0.09	5.16 ± 0.15	4.43 ± 0.07	2.43 ± 0.14	6.38 ± 0.08	7.75 ± 0.21	2.00 ± 0.10	1.00 ± 0.15
22:6n-3*	8.31 ± 0.22	10.71 ± 0.35	9.07 ± 0.18	9.25 ± 0.38	10.54 ± 0.14	4.32 ± 0.14	4.30 ± 0.18	2.10 ± 0.24
Σ SAT	16.31 ± 0.23	14.11 ± 0.43	15.98 ± 0.16	18.30 ± 0.45	11.17 ± 0.20	18.18 ± 0.39	16.78 ± 0.23	16.31 ± 0.53
Σ MUFA	53.62 ± 0.46	55.33 ± 1.01	55.74 ± 0.40	56.61 ± 1.02	55.64 ± 0.34	53.94 ± 0.68	68.79 ± 0.45	74.80 ± 0.91
Σ PUFA	30.07 ± 0.34	30.57 ± 0.72	28.28 ± 0.32	25.09 ± 0.80	33.19 ± 0.26	27.89 ± 0.47	14.44 ± 0.41	8.90 ± 0.70

*Seventeen fatty acids used in MANOVA. SAT = saturated, MUFA = monounsaturated, and PUFA = polyunsaturated.
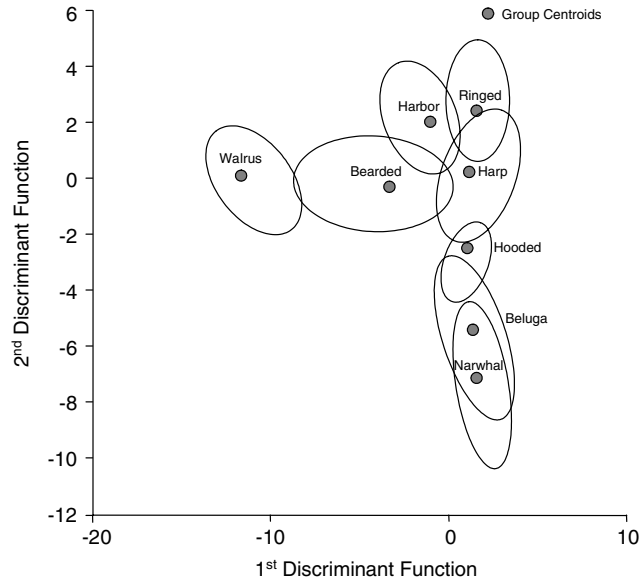
Figure 2. Discriminant analysis of the seventeen most abundant and variable FA in marine mammals sampled across the Canadian Arctic. Discriminant analysis classified 94.4% of original grouped cases and 93.2% of cross-validated grouped cases to the correct species. Ellipses represent 95% data point clouds. Sample sizes are given in Table 1.

Banks Island and Cape Parry were the most distinct. Because bearded seals were sampled in reasonably large numbers in several areas, spatial differences in their FA signatures were tested by MANOVA and discriminant analysis. After pooling samples into broad geographic regions, bearded seal FA signatures differed significantly across the Canadian Arctic (MANOVA on 11 FA: Wilks' $\lambda = 0.083$, $P < 0.001$). Discriminant
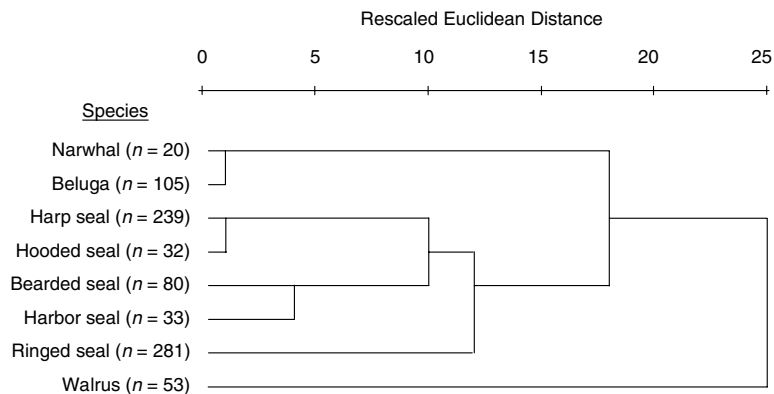
Figure 3. Hierarchical cluster analysis of average FA composition of eight marine mammal species sampled across the Canadian Arctic (Fig. 1). Clustering was based on squared Euclidean distance, using sixty-five FA and the between-groups linkage method.
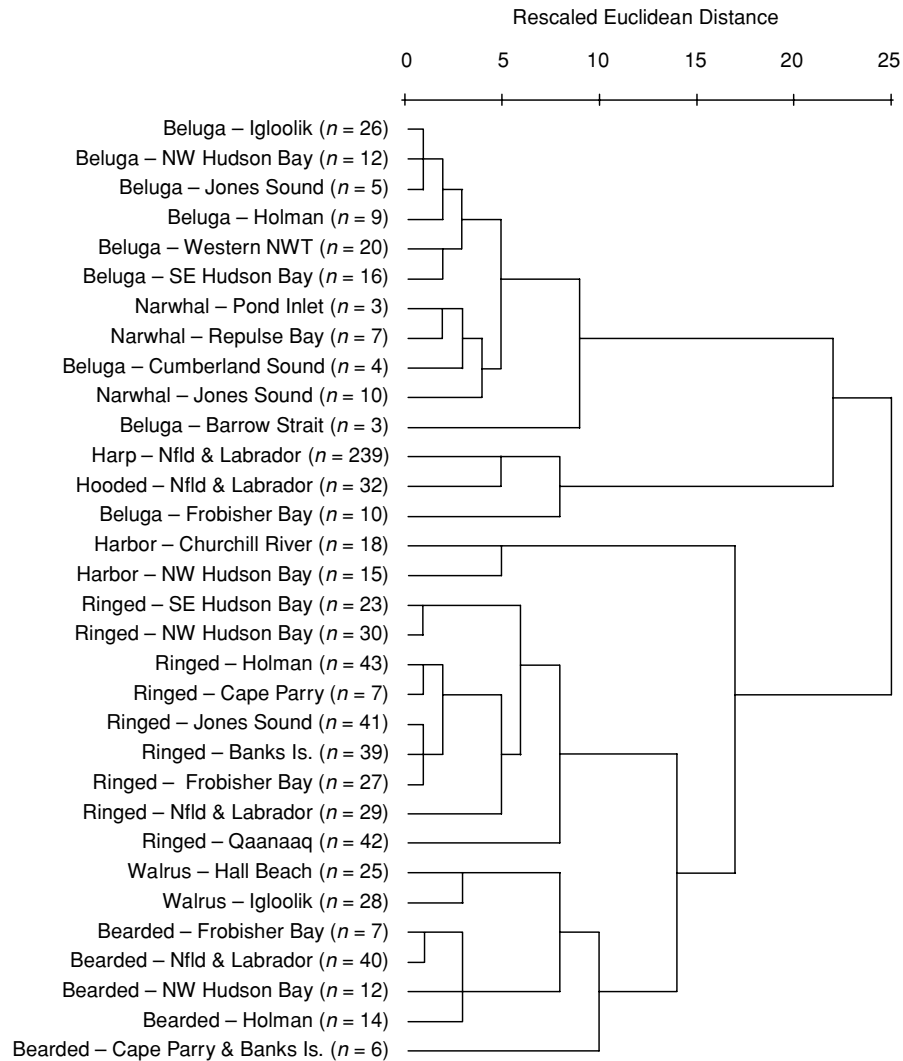
Figure 4. Hierarchical cluster analysis of average FA composition of arctic marine mammals grouped by species and geographic region, and using the same clustering method as for Figure 3.

analysis correctly classified 96.2% of original grouped samples and 89.9% of cross-validated samples to one of the following broad geographic regions: western Hudson Bay, Frobisher Bay/Labrador, or Beaufort Sea-Amundsen Gulf (Fig. 5a).

Beluga whales also showed significant geographic variability in blubber FA composition (MANOVA on 11 FA: Wilks' $\lambda = 0.009$, $P < 0.001$) and discriminant analysis correctly classified 90.9% of original grouped cases and 80.7% of cross-validated grouped cases to one of five geographic regions (Fig. 5b). However, these classification rates were somewhat skewed by the high degree of overlap between northwestern
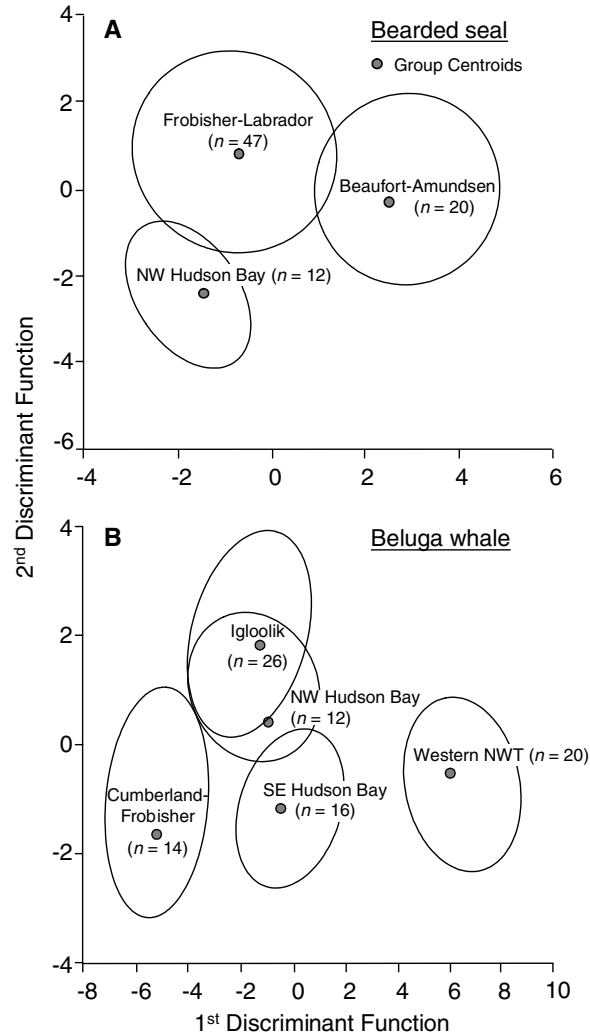
Figure 5.   Discriminant analysis of the eleven most abundant and variable FA in (A) bearded seals in three geographic regions, and (B) beluga whales in five regions. For bearded seals, discriminant analysis classified 96.2% of original grouped cases and 89.9% of cross-validated grouped cases to their correct region. For beluga whales, 90.9% of original grouped cases and 80.7% of cross-validated grouped cases were correctly classified to geographic region. Ellipses represent 95% data point clouds. For bearded seals, a single sample from Jones Sound was not included because of small sample size. For belugas, samples from Jones Sound, Barrow Strait, and Holman were similarly excluded.

Hudson Bay and Igloolik samples; in cross-validation, 19.2% of Igloolik belugas were misclassified to northwestern Hudson Bay, whereas 33.3% of northwestern Hudson Bay belugas were misclassified as Igloolik. Samples from western Northwest Territories (NWT) were correctly classified 100% of the time. In the cluster analysis (Fig. 4), belugas sampled in northwestern Hudson Bay, Igloolik, and Jones Sound

formed a larger group with those sampled in Holman, western NWT, and southeastern Hudson Bay. Cluster analysis clearly separated these groups of belugas from those sampled in Barrow Strait, those in Cumberland Sound (which grouped together with narwhals), and those in Frobisher Bay (which clustered with harp and hooded seals).

Ringed seals from each location grouped together in the overall cluster analysis (Fig. 4). Specific regional trends were previously examined by Thiemann *et al.* (2007*a*), but to summarize, differences in ringed seal FA signatures tended to increase with the geographic distance between groups. Among harbor seals, relatively large sample sizes allowed for a rigorous comparison of geographic variability within the western Hudson Bay region. Seals sampled in northwestern Hudson Bay differed significantly from those sampled at the mouth of the Churchill River (MANOVA on fourteen FA: Wilks' $\lambda = 0.086$, $P < 0.001$; Fig. 6a). Harbor seals in northwestern Hudson Bay had higher levels of 16:0, 20:5n-3, and 22:6n-3, and lower levels of 18:1n-9, 20:1n-11, 20:1n-9, and 20:1n-7 than seals sampled in the Churchill River estuary. Walruses also showed significant variability in FA signatures within a relatively small arctic region (MANOVA on seventeen FA: Wilks' $\lambda = 0.441$, $P = 0.008$; Fig. 6b). Walruses sampled at Hall Beach had higher levels of 16:1n-7, 18:1n-9, and 18:1n-7, and lower levels of 18:4n-3, 20:1n-9, 20:1n-7, 20:5n-3, 22:5n-3, and 22:6n-3 than walruses at Igloolik.
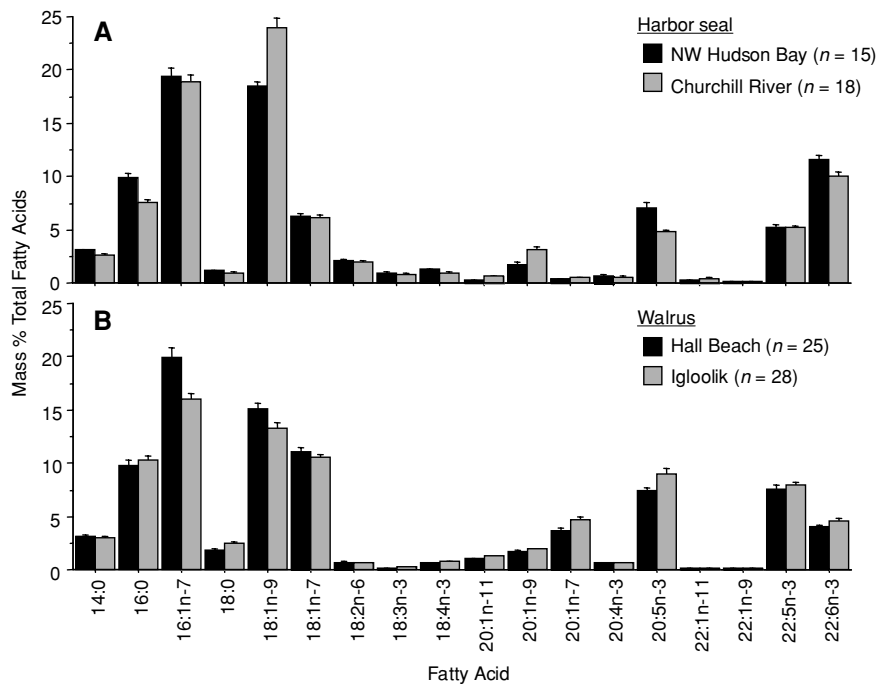

Figure 6. The seventeen most abundant and variable FA, plus 18:0 (mass% of total $+ 1$ SEM) in (A) harbor seals in western Hudson Bay and (B) walruses in Foxe Basin. Location had a significant effect on the FA signature of harbor seals (MANOVA on 14 FA: Wilks' $\lambda = 0.086$, $P < 0.001$) and walruses (MANOVA on seventeen FA: Wilks' $\lambda = 0.441$, $P = 0.008$).

DISCUSSION

Species Differences in Blubber FA Composition

Marine mammal species across the Canadian Arctic were reliably distinguished by their FA signatures (Fig. 2). At the coarsest scale, phocid seals, walruses, and whales were clearly separated from each other with little overlap in the discriminant function plot. The six pinnipeds were also readily distinguished from one another, whereas belugas and narwhals tended to have more similar FA signatures and were often misclassified for each other.

Previous studies have shown that marine mammal FA signatures are largely determined by diet (*e.g.,* Ackman and Eaton 1966; Käkelä *et al*. 1993; Iverson *et al*. 1995, 2004; Kirsch *et al*. 2000) and that spatial differences in blubber composition reflect regional variability in foraging patterns (Iverson *et al*. 1997, Thiemann *et al*. 2007*a*). The differences in FA signatures found in this study were consistent with previous data on species-specific foraging patterns inferred from stomach contents (see references below). However, where stomach content data are lacking, FA signature comparisons can provide unique, longer term, insights into the trophic relationships among marine mammals. For instance, in the eastern Arctic, cluster analyses of FA signatures (Fig. 3, 4) suggest that harp and hooded seal diets are more similar to each other than any other pair of sympatric seal species. Whereas harp seals rely heavily on pelagic fish such as arctic cod (*Boreogadus saida*), polar cod (*Arctogadus glacialis*), and capelin (*Mallotus villosus*), as well as benthic invertebrates and large zooplankton (Sergeant 1976, Finley *et al*. 1990), relatively little is known about the diets of hooded seals aside from an apparent preference for squid and deep water fish such as redfish (*Sebastes marinus*; Sergeant 1976). Our data suggest that the diets of harp and hooded seals may overlap substantially and suggest that the foraging habits of hooded seals warrant further study.

Harp and hooded seals from Newfoundland and Labrador were also grouped to some extent with beluga whales from Frobisher Bay (Fig. 4), indicating some dietary overlap among the three species off southeastern Baffin Island. Although this relationship may have been influenced by sample size (only ten Frobisher belugas were sampled), belugas in other parts of the Arctic are known to feed on a variety of fish and invertebrate species that may also be present in the diets of harp seals, including arctic cod, capelin, squids, and shrimps (Sergeant 1973, Finley *et al*. 1990, Dahl *et al*. 2000, Harwood and Smith 2002).

The other group of Baffin Island belugas, those from nearby Cumberland Sound, did not cluster with harp and hooded seals but rather grouped together with narwhals (Fig. 4). Although narwhals and belugas have similar winter distributions, their dietary similarity is not fully known (Smith 2001). However, the FA signatures of these two species were more similar than any other marine mammals we sampled (Fig. 2, 3), suggesting substantial dietary overlap between the monodontids. Although the similarity between the two whale species in this study may have been affected by evolutionary relatedness, the similarity between beluga whales, harp seals, and hooded seals suggests that trophic relationships, rather than phylogeny, are the driving force behind blubber FA patterns. Furthermore, in our analyses we did not use any of the FA that arise solely from endogenous sources in odontocetes (*e.g.*, Koopman 2007), eliminating that potential phylogenetic influence. The limited stomach content data available indicate that narwhals feed primarily on arctic cod, Greenland halibut (*Reinhardtius hippoglossoides*), polar cod, and, *Gonatus* squid spp. (*e.g.*, Finley

and Gibb 1982, Laidre and Heide-Jørgensen 2005), and where their distributions overlap, narwhals and belugas may therefore share prey populations of arctic cod, polar cod, and squid.

In hierarchical cluster analyses (Fig. 3, 4), ringed seals were clearly separated from all other seal species. Stomach contents indicate that ringed seals feed on a variety of fish including arctic cod, polar cod, and, where available, saffron cod (*Eleginus gracilis*), as well as a wide range of small pelagic invertebrates, most notably the amphipod *Themisto libellula* (*e.g.*, Dunbar 1941; McLaren 1958; Lowry *et al.* 1978, 1980*a,b*; Holst *et al.* 2001). These foraging habits appear to be distinct from the more piscivorous harbor seal (*e.g.*, Baird 2001, Andersen *et al.* 2004) and the primarily benthic-foraging bearded seal (*e.g.*, Lowry *et al.* 1980*a*, Pauly *et al.* 1998). In their comparison of Bering Sea phocids, West *et al.* (1979) also found that ringed seals had the most distinctive FA profile among bearded seals, spotted seals (*Phoca largha*), and ribbon seals (*P. fasciata*). The minor overlap between ringed and harp seal FA signatures indicated by discriminant analysis (Fig. 2) may be related to the common presence, but different proportions, of arctic cod and various small crustacea in the diets of both seals in the eastern Arctic (Dunbar 1941, Sergeant 1976, Finley *et al.* 1990, Holst *et al.* 2001). This overlap may have important implications for future quantitative analyses of polar bear FA signatures, as both ringed and harp seals appear to be important polar bear prey in areas where both species are present (Derocher *et al.* 2002, Iverson *et al.* 2006).

When averaged across all regions, the FA signatures of bearded and harbor seals appeared more similar to each other than to either ringed seals or walruses (Fig. 2, 3). Although this grouping was surprising given the generally different foraging patterns of the two species, a similar overlap in the FA signatures of bearded seals and harbor seals was observed by Iverson *et al.* (2006). Furthermore, Thiemann *et al.* (2007*b*) found evidence that harbor seals in western Hudson Bay may engage in benthic foraging more often than has been reported from other areas. Given that changes in the timing of sea ice breakup in Hudson Bay (Stirling *et al.* 1999, 2004; Gough *et al.* 2004) appear to have contributed to changes in fish populations (Gaston *et al.* 2003) and perhaps even to changes in ringed seal feeding and recruitment (Stirling 2005), increased benthic foraging by harbor seals may be part of a larger, climate-related ecological shift. However, when samples were separated by location (Fig. 4), harbor seals were distinguished from all other species and bearded seals formed a larger cluster with walruses.

Such similarity between bearded seals and walruses is generally more intuitive, given that stomach content analyses indicate that both species feed substantially on benthic invertebrates (Lowry *et al.* 1980*a*, Fisher and Stewart 1997). The significant differences in their overall FA signatures (Fig. 2) may have been influenced by walruses' greater dependence on bivalves such as *Mya truncata*, *Serripes groenlandicus*, and *Hiatella arctica* (Fay 1982, Fisher and Stewart 1997), and bearded seals' significant consumption of shrimps, crabs, and multiple fish species (Lowry *et al.* 1980*a*, Finley and Evans 1983). Using several unusual FA biomarkers, Budge *et al.* (2007) demonstrated similar niche separation in Bering Sea bearded seals and walruses.

Geographic Differences in Blubber FA Composition

Within species, marine mammals in the Canadian Arctic showed significant variability in their FA signatures over large and small spatial scales. However, the differences among groups were also influenced by the distances separating them. For

instance, over large scales, bearded seals could be reliably assigned to their correct geographic region on the basis of their FA signatures (Fig. 5a). However, at smaller spatial scales, cluster analysis (Fig. 4) indicated that bearded seals from two eastern Arctic locations—Frobisher Bay and off the coast of Labrador—were the most similar of any two groups. Although few specific data are available on the diets of eastern Arctic bearded seals, previous analyses of stomach contents have also indicated significant regional variability in bearded seal diets. Finley and Evans (1983) found that bearded seals in the High Arctic fed predominantly on fish, especially sculpins (Cottidae) and arctic cod, whereas invertebrates comprised less than 20% of food items. Conversely, Lowry *et al*. (1980*a*) found that invertebrates dominated the diets of bearded seals in the Bering and Chukchi Seas, and fish typically accounted for less than 20% of total volume of stomach contents. Our results support the overall evidence that bearded seal diets are diverse and regionally variable (see also Hjelset *et al*. 1999).

Although too few narwhals were sampled to rigorously examine regional variability in FA signatures, the relatively tight clustering of narwhals from three widely separated locations (Jones Sound, Pond Inlet, and Repulse Bay) was consistent with evidence that narwhal diets tend to be dominated by only two to three prey species (Finley and Gibb 1982, Laidre and Heide-Jørgensen 2005). In cluster analysis (Fig. 4), narwhals were grouped with belugas from Cumberland Sound, and although sample size was low ($n = 4$), these belugas likely represented a distinct genetic stock that forage in Cumberland Sound and off eastern Baffin Island (de March *et al*. 2002, Innes *et al*. 2002). The narwhals in this study were all sampled during summer; in the fall animals from all three areas migrate to wintering grounds off eastern Baffin Island (Strong 1988, Heide-Jørgensen *et al*. 2002). The similarity of all three groups to beluga whales sampled in this wintering area suggests that winter may be the most important foraging period for narwhals. This conclusion is consistent with Laidre and Heide-Jørgensen's (2005) remarkable observation that narwhals in the eastern Canadian High Arctic had mostly empty stomachs in the summer and showed their greatest food intake during winter months.

Averaged across all regions, the blubber FA composition of beluga whales in the Canadian Arctic (Table 1) was similar to that of belugas near Svalbard (Dahl *et al*. 2000). In both areas, beluga whale blubber was dominated by the monounsaturates 16:1n-7, 18:1n-9, and 20:1n-9, and the saturated FA 14:0 and 16:0. Despite these general similarities between widely separated areas, we found significant regional variability in beluga FA signatures across the Canadian Arctic. Belugas sampled near Igloolik and in northwestern Hudson Bay had the most similar FA signatures and overlapped substantially in the discriminant function plot (Fig. 5b). Although this degree of overlap was surprising considering that the two areas are separated by roughly 1,000 km, individuals in western Hudson Bay have been known to migrate as far north as Repulse Bay (Sergeant 1973), and belugas in both regions may therefore forage in Foxe Basin. The comparatively large difference between belugas in the northwestern and southeastern parts of Hudson Bay (Fig. 4, 5b) further suggests that belugas near the northwestern coast of Hudson Bay do most of their feeding in more northern waters.

The relative differences in FA signatures of beluga whales off southeastern Baffin Island, southeastern Hudson Bay, western NWT, and northwestern Hudson Bay-Foxe Basin (Fig. 5b) were consistent with geographical relationships: The largest difference occurred between the easternmost and westernmost regions and the only overlap occurred between the groups centered around Hudson Bay. Beluga whales in southeastern Baffin Island, southeastern Hudson Bay, western Hudson Bay, and

western NWT each belong to distinct stocks (de March *et al.* 2002, Innes *et al.* 2002, also see Harwood and Smith 2002) and genetic influences on these regional differences cannot be ruled out.

Regional differences in ringed seal FA signatures were examined in detail by Thiemann *et al.* (2007*a*), who found that trends in FA composition were consistent with known differences in ringed seal foraging patterns, as inferred from stomach content and stable isotope analyses. Regional trends in FA signatures were also consistent with geographical relationships, and the largest differences occurred between widely spaced regions (*e.g.*, northwestern Hudson Bay *vs.* Qaanaaq) and the greatest similarity appeared between adjacent groups (*e.g.*, Holman *vs.* Cape Parry).

Harbor seals were only sampled in western Hudson Bay but showed significant FA variability between northwestern Hudson Bay and the Churchill River estuary (Fig. 6a). Iverson *et al.* (1997) found differences in FA signatures and foraging patterns in groups of harbor seals in Prince William Sound separated by as little as 9–15 km. Satellite data from the seals we sampled in northeastern Manitoba indicate that these animals remained within 80 km of the coast during the open water season (Bernhardt *et al.* 2003). Clearly, the localized foraging habits of harbor seals appear to generate localized patterns in their FA signatures. Harbor seals' use of the Churchill River estuary may have been associated with increased foraging on fresh- and brackish-water prey species, relative to the northwestern Hudson Bay seals. Smith *et al.* (1996) found that harbor seals inhabiting a freshwater lake in Quebec had significantly different FA profiles than those in marine habitats in British Columbia, New Brunswick, and Greenland.

Fine-scale differences in FA signatures suggest that walruses at Hall Beach and Igloolik—separated by only 80 km—forage in very localized areas and/or consume different prey species. Fisher and Stewart (1997) examined the stomach contents of walruses in these two locations but presented no evidence of different feeding patterns. However, Outridge and Stewart (1999) found differences in lead isotope ratios and the concentrations of several naturally occurring elements and concluded that the two walrus groups likely forage in different areas. In the absence of adequate sampling of potential prey, FA analysis cannot determine precisely how the diets of Hall Beach and Igloolik walruses differ. However, when considered in the context of stomach content and chemical profile analyses, our data suggest that differences in the FA signatures of these walruses may be a consequence of regional variability in the FA composition of their prey.

The structure and composition of marine mammal blubber may potentially be affected by ontogeny, phylogeny, and thermal regime, in addition to dietary factors (Iverson 2002, Koopman 2007 and references therein). Although we could not account for all of the potential influences on marine mammal blubber, the eight species studied here all inhabit ice-covered arctic waters and are therefore exposed to similar thermal regimes. We found that similarities in foraging ecology translated into similarities in FA profiles, despite sometimes great phylogentic divergence. Because we also did not use any FA in our analyses that are representative of phylogenetic influences (*e.g.*, Budge *et al.* 2006), we therefore conclude that the overall patterns of FA variability presented here are most indicative of trophic relationships and differences among and within species. However, the potential interactive influences of ontogeny and phylogeny with the major effects of diet (ecology) warrant further large-scale study, and we hope that the data presented here can contribute to such future broad-based investigations.

Overall, the FA signatures of the marine mammals studied here were highly consistent with known foraging patterns, as inferred from stomach content and isotope analyses. Our results suggest that species' characteristic foraging patterns generally result in fairly characteristic FA signatures, which can be readily distinguished from other (differently foraging) species. Nevertheless, within these rough, ecologically defined foraging niches of species, there is clearly regional and individual variability, reflecting regional differences in prey and/or foraging patterns of individuals, consistent with other studies of variation in marine mammal foraging. The high degree of accuracy with which discriminant analysis classified individuals to the correct species, as well as the clustering of species sampled in different locations, indicates that regional variability within species, although significant, is much less than the characteristic variability among species. These results validate the use of FA profiles from these predators to determine the diet for an even higher predator (*i.e.*, the polar bear, Iverson *et al.* 2006). That is, these trends, as well as the species-specific FA data presented here, may be used to construct a prey database for future quantitative analyses of the diets of polar bears.

ACKNOWLEDGMENTS

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