

## VARIABILITY IN THE BLUBBER FATTY ACID COMPOSITION OF RINGED SEALS (*PHOCA HISPIDA*) ACROSS THE CANADIAN ARCTIC

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### ABSTRACT

We determined the blubber fatty acid (FA) composition of 281 ringed seals (*Phoca hispida*) across the Canadian Arctic to make inferences about spatial, temporal, and demographic patterns of foraging. Seals were sampled in nine locations between 1992 and 2004. Regional differences in FA signatures were related to the distance between groups, with the greatest similarity occurring among seals sampled in three locations within the Beaufort Sea-Amundsen Gulf. Seals in the western and southeastern portions of Hudson Bay also had similar FA signatures. Discriminant analysis on seventeen FAs classified ringed seals to their correct geographic region with 95% accuracy. Although location accounted for most of the variability in FA signatures, adult and juvenile ringed seals in Frobisher Bay-Labrador Sea and Jones Sound showed significant FA differences, as did male and female ringed seals in Jones Sound and Qaanaaq. Demographic differences were not detected among ringed seals in the Beaufort Sea-Amundsen Gulf or in western Hudson Bay. Seals off the coast of Labrador showed significant seasonal variability in FA signatures. Overall, seasonal, regional, and demographic patterns in FA signatures were consistent with differences in ringed seal diets, as inferred from stomach content and stable isotope analyses.

**Key words:** *Phoca hispida*, ringed seal, blubber, fatty acid signature analysis, foraging, Arctic.

Ringed seals (*Phoca hispida*) are relatively solitary marine carnivores distributed over intermediate water depths throughout the circumpolar Arctic (Maxwell 1967, Kingsley *et al.* 1985). They are dependent on sea ice for molting and for birth of pups, which occurs in lairs that are excavated in snowdrifts above self-maintained breathing

holes in the sea ice (McLaren 1958). Ringed seals feed opportunistically on a variety of fish and small- to medium-sized crustaceans (*e.g.*, Dunbar 1941, McLaren 1958, Lowry *et al.* 1980, Smith 1987, Holst *et al.* 2001) and are, in turn, important prey of both polar bears (*Ursus maritimus*; Stirling 1974, Stirling and Archibald 1977, Smith 1980) and arctic foxes (*Alopex lagopus*; Smith 1976). Because of their high abundance, ubiquitous distribution, and central position in the food web, ringed seals play an important role in the dynamics of arctic marine ecosystems (Smith *et al.* 1991). Changes in ringed seal populations can reflect large-scale changes in ice conditions and/or food supply (*e.g.*, Stirling 2002), and recent declines in ringed seal reproduction may be a consequence of earlier sea ice breakup, decreasing snow cover, and likely other unknown ecological factors (Ferguson *et al.* 2005, Stirling 2005).

Lipids, and fatty acids (FAs) in particular, can serve as biological markers and indicators of trophic relationships in marine food webs (Brockerhoff *et al.* 1967, Sargent *et al.* 1987, Kharlamenko *et al.* 1995, Iverson *et al.* 1997, Bradshaw *et al.* 2003). Marine ecosystems contain a wide array of FAs, and limitations on the synthesis of FAs in mammalian predators result in many dietary FAs being directly, or at least predictably, incorporated into consumer tissue (*e.g.*, Ackman and Eaton 1966, Iverson *et al.* 1995, Dalsgaard and St. John 2004). The relative abundance of multiple FAs (*i.e.*, a FA signature) in the adipose stores of a predator can therefore provide information on diet integrated over a span of weeks to months (*e.g.*, Kirsch *et al.* 2000, Iverson *et al.* 2004). When incorporated into a mathematical model, predator and prey FA signatures can be used to produce a quantitative estimate of the predator's diet composition (Iverson *et al.* 2004, 2006). In the absence of extensive prey sampling, trends in predator FA signatures can be used to detect spatial, temporal, and demographic differences in foraging (*e.g.*, Iverson *et al.* 1997, Beck *et al.* 2005, Budge *et al.* 2006).

Few studies have examined the FA composition of ringed seal blubber (West *et al.* 1979, Iverson *et al.* 2006). Käkälä *et al.* (1993, 1995), and Käkälä and Hyvärinen (1998) observed differences in FA composition among ringed seals inhabiting marine, brackish, and freshwater environments in northern Europe and concluded that the composition of ringed seal blubber reflected dietary intake. However, no studies have examined regional and demographic variability in arctic marine habitats and how such trends in ringed seal FAs are related to known foraging habits. We analyzed ringed seal blubber samples collected across the Canadian Arctic over a 13-yr period to (1) investigate how FA signatures vary between regions, among demographic groups, and over time; (2) examine the relationship between trends in FA signatures and trends in ringed seal foraging, as inferred from stomach content and stable isotope analyses; and (3) establish baseline data that can inform future studies on the effects of environmental change on this important arctic species. In addition, these data will be essential for future FA examinations of the role of ringed seals in the diets of polar bears and other arctic predators.

## METHODS

### *Sample Collection*

Blubber samples were collected from 281 ringed seals across the Canadian Arctic between 1992 and 2004 (Fig. 1, Table 1). In all areas, seals were shot nonselectively by Inuit hunters or sampled by other researchers studying ringed seal ecology with the result that animals of all age and sex classes were represented. Ages were determined

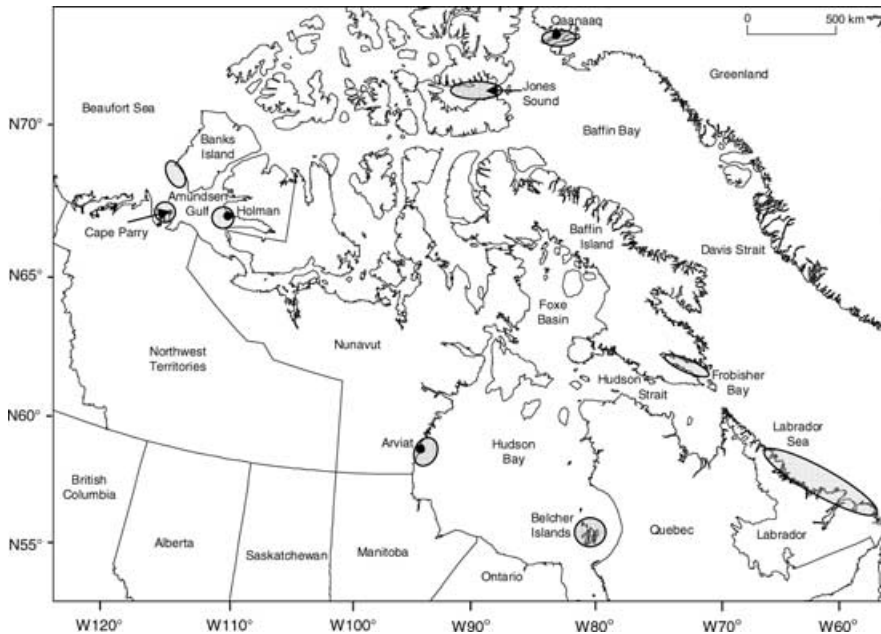


Figure 1. Locations of ringed seals sampled between 1992 and 2004. For some analyses, seals from the Beaufort Sea and Amundsen Gulf were pooled (Beaufort-Amundsen), as were seals from Frobisher Bay and the coast of Labrador (Frobisher-Labrador).

by counting cementum growth layer groups in canine teeth extracted from the lower jaw (Stewart *et al.* 1996). Seals 6 yr and older were considered adults (McLaren 1958; Smith 1973, 1987) and those between 3 and 5 yr were considered subadults (see Table 1).

To examine fine-scale regional variability of ringed seal FA signatures within large contiguous water bodies, samples were compared from discrete locations within southeastern Beaufort Sea/Amundsen Gulf, and Davis Strait/Labrador Sea (Fig. 1). For larger-scale regional comparisons, seals from the Beaufort Sea and Amundsen Gulf were pooled together (Beaufort-Amundsen), as were seals from Frobisher Bay and the coast of Labrador (Frobisher-Labrador). To facilitate a preliminary analysis of seasonal differences in FA composition, samples from juvenile seals collected from 1994 to 1997 off the Labrador coast in both fall (September) and winter (November–February) were compared. Because seals were sampled opportunistically across a vast geographic area, often only a few samples were available from a given location in a given year. Although too few samples were available to rigorously test for interannual differences, where possible, we removed the possibility of confounding interannual effects by examining regional and demographic trends among samples collected in a single year.

To examine the relationship between FA signatures and diet, we compared spatial and demographic trends in FA signatures to trends in stomach contents from the seals sampled at Qaanaaq and Jones Sound (complete stomach content data are presented in Holst *et al.* 2001). Although stomach contents were not available for individuals sampled in other regions, previous studies have examined the diets of ringed seals in

Table 1. Distribution of young-of-the-year (YOY), yearling (YRLG) and 2-yr-old (2-YR), subadult (3–5 yr), and adult (6+ yr) ringed seals sampled with respect to temporal distribution, location (see Fig. 1), and sex.

Region	Sampling period	Year	Total	YOY						YRLG and 2-YR						Subadult			Adult			No age			
				F		M		F		M		F		M		F		M		F		M		U*	
Labrador	Sep, Nov–Feb	1994–1997	29	1	6	4	0	0	4	10	4	3	1	0	0	0	0	0	0	0	0	0	0		
Frobisher Bay	Aug–Sep	1998, 2000	27	3	5	0	0	0	0	0	0	12	5	2	0	0	0	0	0	0	0	0	0		
Belcher Islands	Mar	2003	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23			
Arviat	Sep–Oct	1992, 1998	30	0	1	0	2	3	6	10	8	0	0	0	0	0	0	0	0	0	0	0	0		
Qaanaaq	May–Jun	1998	42	2	1	0	0	13	12	5	9	0	0	0	0	0	0	0	0	0	0	0	0		
Jones Sound	May–Jun	1998	41	6	5	1	0	0	0	0	15	13	0	1	0	0	0	0	0	0	0	0	0		
Holman	Jun–Aug	1996, 1999, 2001	43	0	0	0	1	1	2	21	18	0	0	0	0	0	0	0	0	0	0	0	0		
Banks Island	May–Jul	2001, 2004	39	1	0	1	2	4	7	10	13	1	0	0	0	0	0	0	0	0	0	0	0		
Cape Parry	May–Sep	1995, 2004	7	2	0	0	0	2	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0		
Total			281	15	18	6	5	27	38	77	67	4	1	4	1	23	0	0	0	0	0	0	0		

\*Sex data unavailable.

many of these areas, including coastal Baffin Island (Dunbar 1941, McLaren 1958), Baffin Bay (Finley *et al.* 1983, Siegstad *et al.* 1998), Davis Strait (Siegstad *et al.* 1998), and the Beaufort Sea (Lowry *et al.* 1978, 1980).

### *Lipid and Statistical Analyses*

Large samples of blubber (approximately  $8 \times 8$  cm) extending through the depth of the adipose layer and including a portion of attached subcutaneous (panniculus) muscle to facilitate vertical orientation were collected from each seal. Samples were collected from the midflank region where the blubber is the thickest (Ryg *et al.* 1988) shortly ( $<ca.$  2 h) after death, wrapped in foil, and stored at  $-20^{\circ}\text{C}$ . 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 subject to little degradation during frozen storage (Budge *et al.* 2006).

Lipid was extracted and isolated from each biopsy subsample according to Iverson *et al.* (2001) and FA methyl esters (FAME) prepared from each lipid sample using an acidic catalyst (the Hilditch method; Hilditch and Williams 1964, Thiemann *et al.* 2004). 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), with each FA expressed as the weight percent of total FAs  $\pm$  SEM. Identified FAs are referred to by the standard nomenclature of carbon chain length:number of double bonds, and location ( $n - x$ ) of the double bond nearest to the terminal methyl group (IUPAC-IUB 1967).

The values of the seventeen most abundant and/or most variable FAs were transformed to improve normality by calculating the log of the ratio of each FA to 18:0 (Budge *et al.* 2002, 2006; Iverson *et al.* 2002). The seventeen FAs included those that were highly abundant in ringed seal blubber as well as several important dietary FAs (Iverson *et al.* 2004). A combination of discriminant analysis, multivariate analysis of variance (MANOVA), and hierarchical cluster analysis (SPSS 1997, Budge *et al.* 2006) was used to examine variability in ringed seal FA signatures by region, age, sex, and season. Original and cross-validated classification rates were used to assess the ability of discriminant analyses to distinguish groups of seals based on their FA signatures. Cross-validation was performed by classifying each seal against the functions derived from all other seals. Within most regions, age- and sex-specific differences were tested by two-way MANOVA. Three-way MANOVA was used to incorporate regional and demographic (*i.e.*, age and sex) variability when comparisons were made within Beaufort-Amundsen, within Frobisher-Labrador, between Jones Sound and Qaanaaq, or across all regions. One-way MANOVA was used to test for seasonal differences among seals of the same age class in the Labrador Sea. Because the sample size of any group must exceed the number of response variables tested by MANOVA or discriminant analysis (Stevens 1986, Legendre and Legendre 1998), smaller subsets of FAs (minimum of 10) were used in some analyses. To achieve a minimum sample size of eleven, seals  $<6$  yr were pooled into a single "juvenile" age category in some regions. For hierarchical cluster analysis, the number of variables is not limited by sample size, and consequently, cluster analysis was performed using all identified FAs.

## RESULTS

Approximately sixty-five FAs were routinely identified and quantified in ringed seal blubber samples. Table 2 lists the thirty-nine FAs that averaged  $>0.1\%$  across

Table 2. Fatty acid composition and major lipid classes (mass % of total FAs ± SEM) of blubber samples collected from ringed seals across the Canadian Arctic. Although sixty-five FAs were identified and quantified in most samples, only the thirty-nine FAs that averaged >0.1% across all regions are listed.

Region: n:	Labrador 29	Frobisher Bay 27	Belcher Islands 23	Arviat 30	Qaanaaq 42	Jones Sound 41	Holman 43	Banks Island 39	Cape Parry 7
SAT									
14:0*	4.91 ± 0.16	3.99 ± 0.13	4.87 ± 0.22	4.18 ± 0.14	3.84 ± 0.09	3.13 ± 0.10	3.30 ± 0.10	2.80 ± 0.09	3.72 ± 0.39
15:0	0.24 ± 0.01	0.20 ± 0.01	0.31 ± 0.01	0.26 ± 0.01	0.19 ± 0.01	0.13 ± 0.01	0.18 ± 0.00	0.17 ± 0.01	0.21 ± 0.02
Iso15	0.14 ± 0.01	0.14 ± 0.01	0.20 ± 0.01	0.20 ± 0.01	0.15 ± 0.00	0.12 ± 0.00	0.13 ± 0.00	0.12 ± 0.00	0.14 ± 0.01
16:0*	7.04 ± 0.21	5.97 ± 0.29	8.31 ± 0.41	7.35 ± 0.36	5.87 ± 0.20	4.17 ± 0.24	4.48 ± 0.19	4.20 ± 0.22	5.81 ± 0.88
7Me16:0	0.28 ± 0.00	0.28 ± 0.01	0.41 ± 0.01	0.38 ± 0.01	0.27 ± 0.00	0.25 ± 0.00	0.28 ± 0.01	0.28 ± 0.01	0.33 ± 0.01
Iso17	0.09 ± 0.01	0.11 ± 0.01	0.15 ± 0.01	0.15 ± 0.01	0.11 ± 0.00	0.07 ± 0.00	0.08 ± 0.00	0.10 ± 0.01	0.11 ± 0.01
18:0	0.65 ± 0.02	0.64 ± 0.05	0.83 ± 0.04	0.76 ± 0.04	0.76 ± 0.04	0.46 ± 0.03	0.54 ± 0.03	0.53 ± 0.04	0.63 ± 0.10
MUFA									
14:1n-9	0.12 ± 0.01	0.11 ± 0.01	0.18 ± 0.02	0.16 ± 0.01	0.19 ± 0.01	0.22 ± 0.01	0.24 ± 0.01	0.15 ± 0.01	0.19 ± 0.01
14:1n-5	0.96 ± 0.05	1.16 ± 0.06	1.29 ± 0.07	1.48 ± 0.11	0.79 ± 0.06	1.55 ± 0.07	1.31 ± 0.08	1.38 ± 0.07	1.10 ± 0.28
16:1n-11	0.50 ± 0.02	0.55 ± 0.03	0.42 ± 0.01	0.45 ± 0.01	0.63 ± 0.02	0.72 ± 0.02	0.56 ± 0.02	0.62 ± 0.03	0.58 ± 0.10
16:1n-9	0.30 ± 0.02	0.45 ± 0.02	0.32 ± 0.01	0.41 ± 0.02	0.49 ± 0.03	0.71 ± 0.02	0.53 ± 0.02	0.56 ± 0.02	0.52 ± 0.12
16:1n-7*	20.49 ± 0.76	20.05 ± 0.65	18.73 ± 0.61	18.48 ± 0.35	16.00 ± 0.41	19.97 ± 0.38	18.48 ± 0.47	20.27 ± 0.46	19.43 ± 0.72
17:1	0.18 ± 0.02	0.24 ± 0.02	0.25 ± 0.02	0.28 ± 0.02	0.20 ± 0.02	0.13 ± 0.00	0.16 ± 0.01	0.23 ± 0.01	0.19 ± 0.02
18:1n-11	2.14 ± 0.15	2.68 ± 0.22	1.09 ± 0.08	1.20 ± 0.11	4.60 ± 0.15	5.17 ± 0.21	4.08 ± 0.23	3.86 ± 0.22	2.81 ± 0.38
18:1n-9*	10.17 ± 0.40	15.44 ± 0.54	12.93 ± 0.33	14.19 ± 0.34	11.34 ± 0.46	15.11 ± 0.25	12.85 ± 0.33	14.78 ± 0.51	12.77 ± 1.45
18:1n-7*	3.67 ± 0.11	4.47 ± 0.21	5.08 ± 0.25	4.87 ± 0.15	3.57 ± 0.10	4.22 ± 0.13	3.88 ± 0.06	4.68 ± 0.15	4.25 ± 0.12
18:1n-5	0.49 ± 0.02	0.59 ± 0.02	0.61 ± 0.03	0.76 ± 0.02	0.55 ± 0.01	0.47 ± 0.01	0.52 ± 0.01	0.52 ± 0.02	0.57 ± 0.03
20:1n-11*	1.06 ± 0.07	1.57 ± 0.15	0.57 ± 0.04	0.58 ± 0.04	2.02 ± 0.08	2.09 ± 0.10	1.72 ± 0.10	1.54 ± 0.08	1.00 ± 0.10
20:1n-9*	6.70 ± 0.38	7.12 ± 0.48	3.77 ± 0.36	4.67 ± 0.33	11.63 ± 0.56	7.87 ± 0.35	9.02 ± 0.44	6.98 ± 0.37	7.23 ± 0.66
20:1n-7*	0.49 ± 0.02	0.49 ± 0.02	0.40 ± 0.05	0.50 ± 0.02	0.80 ± 0.04	0.64 ± 0.03	0.83 ± 0.06	0.74 ± 0.05	0.67 ± 0.09
22:1n-11*	2.55 ± 0.23	1.46 ± 0.18	0.84 ± 0.15	1.09 ± 0.14	3.28 ± 0.31	1.03 ± 0.09	1.86 ± 0.18	1.28 ± 0.20	2.27 ± 0.47
22:1n-9*	0.45 ± 0.03	0.35 ± 0.03	0.19 ± 0.02	0.31 ± 0.03	0.97 ± 0.08	0.48 ± 0.04	0.71 ± 0.07	0.46 ± 0.05	0.56 ± 0.10

Table 2. Continued.

PUFA													
16:2n-4	0.09 ± 0.01	0.10 ± 0.01	0.22 ± 0.02	0.29 ± 0.02	0.11 ± 0.01	0.08 ± 0.00	0.17 ± 0.01	0.15 ± 0.00	0.15 ± 0.01				
16:3n-6	0.69 ± 0.02	0.54 ± 0.02	0.67 ± 0.04	0.44 ± 0.02	0.58 ± 0.02	0.80 ± 0.02	0.74 ± 0.02	0.66 ± 0.02	0.75 ± 0.03				
16:3n-4	0.50 ± 0.04	0.25 ± 0.02	0.34 ± 0.02	0.20 ± 0.01	0.24 ± 0.01	0.27 ± 0.02	0.35 ± 0.02	0.25 ± 0.01	0.44 ± 0.05				
16:4n-1	0.98 ± 0.07	0.49 ± 0.07	0.39 ± 0.02	0.25 ± 0.02	0.43 ± 0.03	0.36 ± 0.05	0.38 ± 0.03	0.28 ± 0.02	0.48 ± 0.09				
18:2n-6*	1.66 ± 0.09	1.65 ± 0.08	1.17 ± 0.05	1.84 ± 0.05	1.10 ± 0.04	0.77 ± 0.01	0.92 ± 0.03	0.92 ± 0.04	1.00 ± 0.04				
18:2n-4	0.13 ± 0.00	0.14 ± 0.00	0.12 ± 0.01	0.10 ± 0.00	0.10 ± 0.00	0.12 ± 0.01	0.12 ± 0.00	0.11 ± 0.00	0.15 ± 0.01				
18:3n-6	0.19 ± 0.01	0.20 ± 0.01	0.12 ± 0.00	0.11 ± 0.01	0.15 ± 0.01	0.17 ± 0.01	0.16 ± 0.01	0.18 ± 0.01	0.18 ± 0.02				
18:3n-3*	0.48 ± 0.03	0.37 ± 0.02	0.58 ± 0.03	0.62 ± 0.04	0.34 ± 0.01	0.25 ± 0.01	0.44 ± 0.01	0.44 ± 0.02	0.43 ± 0.04				
18:4n-3*	1.72 ± 0.06	1.32 ± 0.07	1.27 ± 0.07	1.27 ± 0.09	0.89 ± 0.04	0.60 ± 0.05	0.96 ± 0.05	0.89 ± 0.04	1.23 ± 0.12				
18:4n-1	0.26 ± 0.01	0.20 ± 0.01	0.09 ± 0.01	0.08 ± 0.01	0.15 ± 0.01	0.16 ± 0.01	0.13 ± 0.01	0.14 ± 0.01	0.17 ± 0.01				
20:2n-6	0.22 ± 0.01	0.25 ± 0.01	0.17 ± 0.01	0.25 ± 0.01	0.19 ± 0.01	0.15 ± 0.01	0.20 ± 0.01	0.21 ± 0.01	0.22 ± 0.01				
20:4n-6	0.32 ± 0.02	0.37 ± 0.03	0.38 ± 0.04	0.43 ± 0.05	0.34 ± 0.01	0.40 ± 0.02	0.30 ± 0.01	0.43 ± 0.02	0.39 ± 0.05				
20:4n-3*	0.42 ± 0.01	0.41 ± 0.02	0.41 ± 0.03	0.46 ± 0.03	0.35 ± 0.01	0.28 ± 0.01	0.40 ± 0.01	0.40 ± 0.01	0.42 ± 0.01				
20:5n-3*	11.98 ± 0.36	9.12 ± 0.28	10.86 ± 0.41	9.44 ± 0.28	8.86 ± 0.34	8.99 ± 0.23	8.67 ± 0.32	8.75 ± 0.37	10.02 ± 0.34				
21:5n-3	0.47 ± 0.01	0.45 ± 0.01	0.43 ± 0.01	0.38 ± 0.01	0.37 ± 0.01	0.39 ± 0.01	0.39 ± 0.01	0.37 ± 0.01	0.39 ± 0.01				
22:5n-3*	5.78 ± 0.18	5.51 ± 0.12	5.80 ± 0.21	5.72 ± 0.20	6.67 ± 0.18	6.96 ± 0.20	6.86 ± 0.16	6.82 ± 0.27	6.33 ± 0.23				
22:6n-3*	8.88 ± 0.33	9.04 ± 0.34	13.10 ± 0.56	13.32 ± 0.40	9.23 ± 0.16	9.19 ± 0.18	11.49 ± 0.22	11.02 ± 0.32	10.33 ± 0.34				
Σ SAT	13.85 ± 0.35	11.73 ± 0.43	15.66 ± 0.59	13.78 ± 0.49	11.57 ± 0.31	8.58 ± 0.36	9.26 ± 0.30	8.49 ± 0.35	11.28 ± 1.40				
Σ MUFA	50.69 ± 0.68	57.11 ± 0.80	47.21 ± 0.46	49.99 ± 0.74	57.57 ± 0.61	60.81 ± 0.50	57.23 ± 0.64	58.54 ± 0.65	54.63 ± 1.80				
Σ PUFA	35.46 ± 0.68	31.16 ± 0.54	37.13 ± 0.61	36.23 ± 0.66	30.86 ± 0.57	30.62 ± 0.46	33.51 ± 0.60	32.97 ± 0.87	34.08 ± 0.70				

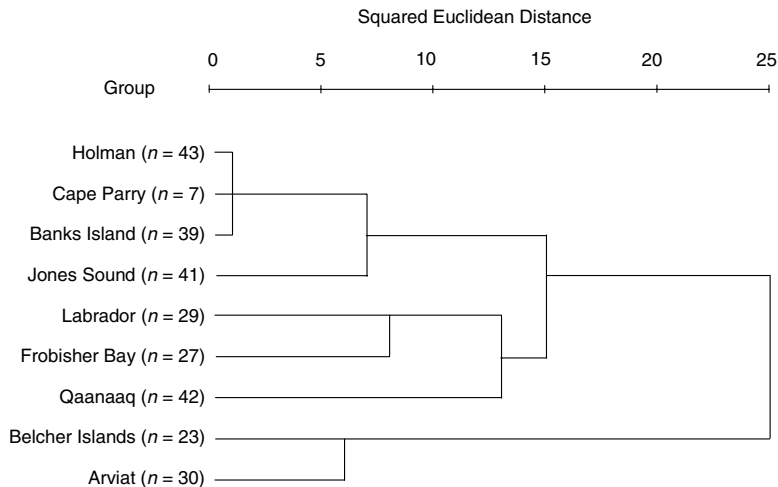
\* 17 fatty acids used in MANOVA and discriminant analyses. SAT = saturated FA, MUFA = monounsaturated FA, PUFA = polyunsaturated FA.

all regions. The seventeen FAs used in statistical analyses accounted for 91.3% of total FAs across all areas.

### *Regional Variability*

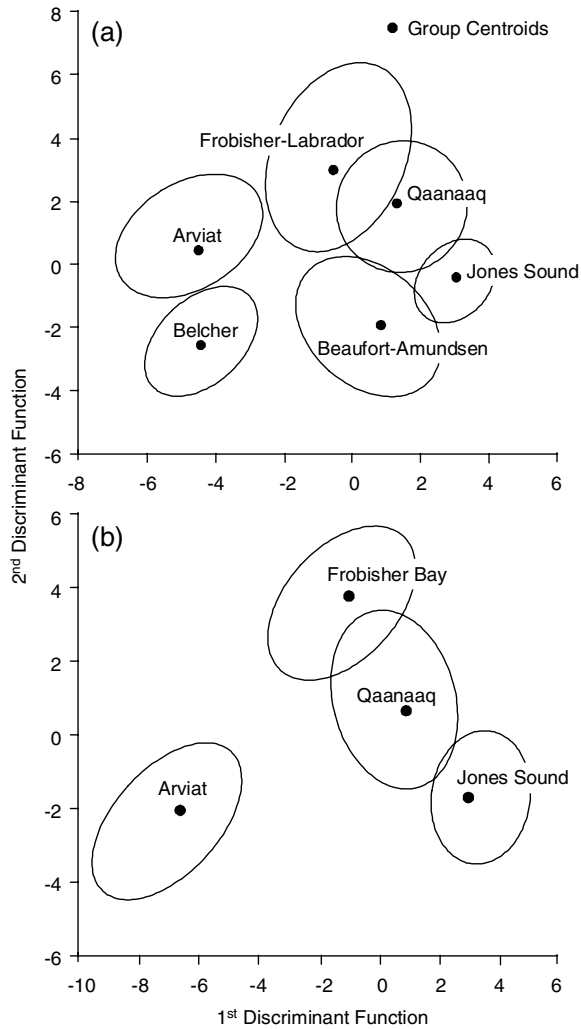
Exploratory hierarchical cluster analysis indicated that patterns of ringed seal FA signatures were related to the geographic distance between groups (Fig. 2). Specifically, seals sampled within the Beaufort-Amundsen region showed the greatest similarity of any groups. Ringed seals sampled in two areas of Hudson Bay also clustered together, as did those from Frobisher Bay and the coast of Labrador. At the largest scale, hierarchical cluster analysis separated the two Hudson Bay areas from all other groups of seals. Given the similarity of FA signatures within Beaufort-Amundsen and Frobisher-Labrador, samples within these two regions were pooled to increase sample sizes for MANOVA and discriminant analysis.

When tested by three-way MANOVA to remove potential age and sex effects, ringed seals showed significant regional differences in FA composition (Wilks'  $\lambda = 0.010$ ,  $P < 0.001$ ), with each of the seventeen FAs differing significantly across geographic regions. Discriminant analysis (Fig. 3a) classified 95.0% of original cases and 92.5% of cross-validated cases to their correct region, with samples from Qaanaaq being the most commonly misclassified. Six of the forty-two Qaanaaq samples were incorrectly classified; two were classified as being from Frobisher-Labrador, two as Jones Sound, and one each as being from Arviat and Beaufort-Amundsen. All thirty samples from Arviat were correctly identified. The first and second discriminant functions accounted for 80% of total variance, and the only substantial overlap in the discriminant function plot occurred between Frobisher-Labrador and Qaanaaq seals. To eliminate the potential influence of interannual effects on regional trends,



*Figure 2.* Hierarchical cluster analysis of average ringed seal FA composition in nine geographic regions. Clusters were formed based on squared Euclidean distance, using sixty-four FAs and the between-groups linkage method. Cluster analysis indicates that differences in FA signatures tended to increase with geographic distance.



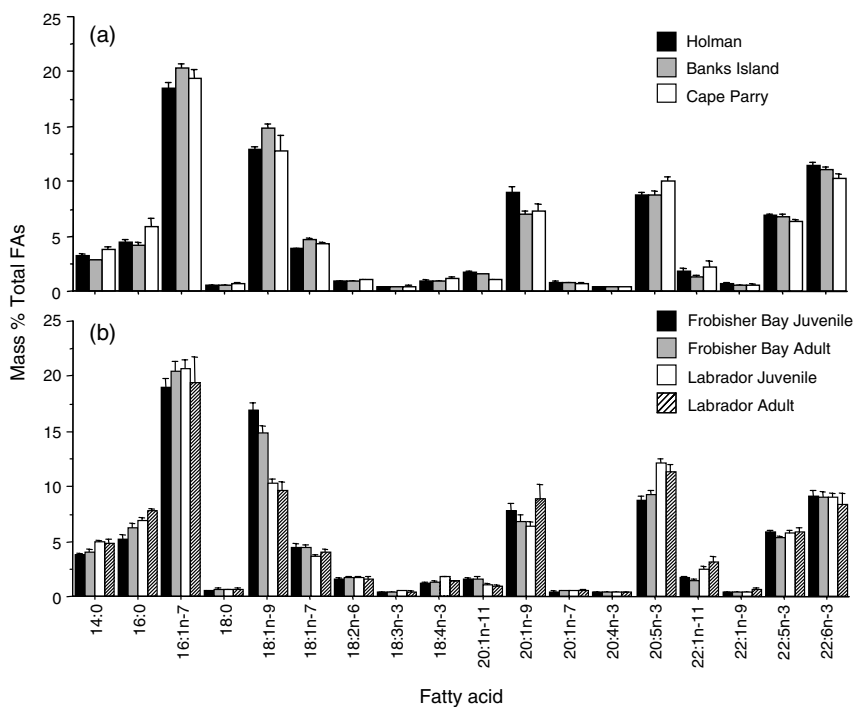


*Figure 3.* Discriminant analysis of ringed seals in major geographic regions using the seventeen most abundant and variable FAs measured in (a) all seals in all years and (b) seals sampled in 1998. The Beaufort-Amundsen group includes all seals from Cape Parry, Banks Island, and Holman. Across all years, discriminant analysis correctly classified 95.0% of original grouped cases and 92.5% of cross-validated grouped cases to their correct region. Among seals sampled in 1998, original and cross-validated samples were classified with 96.1% and 91.4% accuracy, respectively. Ellipses represent 95% data point clouds. See Table 1 for sample sizes.

we repeated the discriminant analysis using only those samples collected in 1998 (Fig. 3b). In this analysis, the first two discriminant functions accounted for 92.2% of total variance and original and cross-validated samples were classified with 96.1% and 91.4% accuracy, respectively. Overall, limiting samples to those collected in a single year appeared to make regional differences more pronounced.

To examine spatial variability among seals in Beaufort-Amundsen, those from the western portion of the study area (*i.e.*, Banks Island and Cape Parry; see Fig. 1) were pooled and tested against those from the eastern region (*i.e.*, Holman). Comparison by three-way MANOVA across age, sex, and location indicated significant east-west variability (Wilks'  $\lambda = 0.663$ ,  $P = 0.036$ ; Fig. 4a). When the seven seals from Cape Parry were excluded and the analysis was limited to the well-represented Banks Island and Holman groups, east-west differences were more pronounced (Wilks'  $\lambda = 0.497$ ,  $P < 0.001$ ). Seals near Holman had higher levels of 14:0, 20:1n-9, 22:1n-11, and 22:1n-9 and lower levels of 18:1n-9 and 18:1n-7 than seals near Banks Island. When the comparison was limited to seals sampled in 2001 to remove any year-to-year variability, differences between Holman ( $n = 22$ ) and Banks Island ( $n = 22$ ) became even larger (Wilks'  $\lambda = 0.159$ ,  $P < 0.001$ ). In addition to differences in 20:1n-9, 22:1n-11, and 22:1n-9, Holman seals had higher levels of 20:1n-11, 22:5n-3, and 22:6n-3.

Significant fine-scale regional variability was also evident in the eastern Arctic where seals off the coast of Labrador had significantly different FA profiles than those



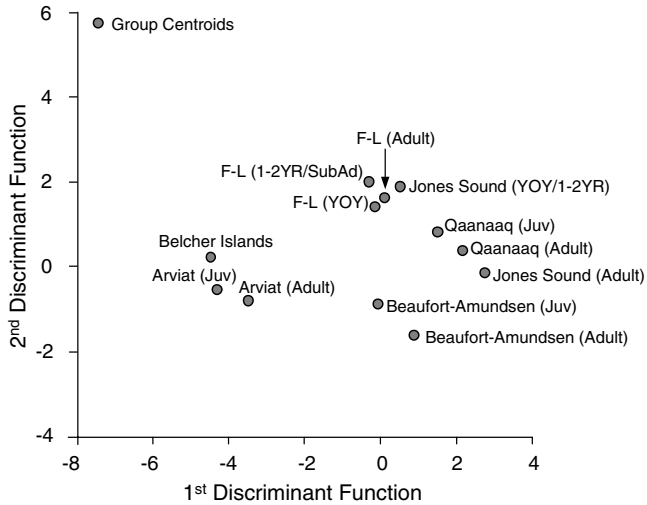
**Figure 4.** The seventeen most abundant and variable FAs, plus 18:0 (mass % of total + 1 SEM) of ringed seals sampled in (a) Beaufort-Amundsen and (b) Frobisher-Labrador. To increase the power of MANOVA, samples from the western portion of the Beaufort-Amundsen study area (*i.e.*, Banks Island,  $n = 39$  and Cape Parry,  $n = 7$ ) were pooled and compared to the eastern samples (*i.e.*, Holman,  $n = 43$ ); location had a significant effect on ringed seal FA signatures in this area ( $P = 0.036$ ). FA signatures also differed between Frobisher Bay ( $n = 27$ ) and the Labrador coast ( $n = 29$ ;  $P < 0.001$ ) and between adults ( $n = 23$ ) and juveniles ( $n = 33$ ) within this region ( $P = 0.050$ ).

in Frobisher Bay (MANOVA: Wilks'  $\lambda = 0.190$ ,  $P < 0.001$ ; Fig. 4b). Baffin Island ringed seals had higher levels of 18:1n-9, 18:1n-7, and 20:1n-11, whereas Labrador seals had greater levels of 16:0, 18:4n-3, 20:5n-3, 22:1n-11, and 22:1n-9. However, because Labrador and Frobisher Bay seals were sampled in different years (Table 1), the possibility of confounding interannual effects could not be eliminated.

### Demographic Variability

Across all regions, ringed seal FA signatures differed by age class (MANOVA: Wilks'  $\lambda = 0.653$ ,  $P < 0.001$ ) but not by sex (Wilks'  $\lambda = 0.921$ ,  $P = 0.356$ ). Adult and juvenile ringed seals across the Canadian Arctic differed for thirteen of the seventeen FAs tested by MANOVA. To examine the relative influence of age on FA signatures in different regions, discriminant analysis was performed on eleven FAs (*i.e.*, smallest sample size minus 1). Overall, 66.1% of original cases and 52.9% of cross-validated cases were classified to their correct region and age class, and the first two discriminant functions accounted for 82.4% of total variance (Fig. 5). Although the classification rate to age class and region was relatively poor, seals of different ages tended to group together by region. Ringed seals in Jones Sound showed the greatest age class separation.

In Frobisher-Labrador, ringed seal FA signatures differed by age class (MANOVA: Wilks'  $\lambda = 0.472$ ,  $P = 0.050$ ; Fig. 4b) but not by sex (Wilks'  $\lambda = 0.735$ ,  $P = 0.835$ ).



*Figure 5.* Plot of the group centroids (within-group mean for each discriminant function) of different age classes of ringed seals in six geographic regions, using the eleven most abundant and variable FAs. Beaufort-Amundsen includes all seals from Cape Parry, Banks Island, and Holman, whereas the F-L group comprises seals from Frobisher Bay and the coast of Labrador. The first and second discriminant functions accounted for 82.4% of total variance. Discriminant analysis classified 66.1% of original grouped cases and 52.9% of cross-validated grouped cases to their correct age class and region. No age data were available for ringed seals from Belcher Islands. See Table 1 for sample sizes and age class definitions. Juv = all juvenile age classes available.

Juvenile and adult ringed seals differed in their relative levels of 14:0, 16:0, 18:3n-3, 18:4n-3, 20:5n-3, and 22:1n-11. There was a significant interactive effect between age class and sampling area within Frobisher-Labrador (Wilks'  $\lambda = 0.283$ ,  $P < 0.001$ ) indicating that age trends were not consistent in the two areas.

There were no age- or sex-related differences in FA signatures among ringed seals sampled at Arviat (sex: Wilks'  $\lambda = 0.764$ ,  $P = 0.865$ ; age class: Wilks'  $\lambda = 0.532$ ,  $P = 0.290$ ) or Beaufort-Amundsen (sex: Wilks'  $\lambda = 0.775$ ,  $P = 0.396$ ; age class: Wilks'  $\lambda = 0.683$ ,  $P = 0.061$ ). In Jones Sound, where all samples were collected in 1998, FA signatures differed by both age (MANOVA on eleven FAs: Wilks'  $\lambda = 0.085$ ,  $P < 0.001$ ) and sex (Wilks'  $\lambda = 0.438$ ,  $P = 0.010$ ; Fig. 6a). Age had a significant effect on the relative levels of 16:0, 16:1n-7, 18:1n-9, 20:1n-11, 20:1n-9, 20:5n-3, 22:1n-11, 22:5n-3, and 22:6n-3, whereas only 22:5n-3 differed between the sexes. There was also a statistically significant age-sex interaction (Wilks'  $\lambda = 0.453$ ,  $P = 0.014$ ) that resulted from variable age trends among the sexes. For instance, males had greater levels of 22:5n-3 and 22:6n-3 among juveniles but lower levels among adults.

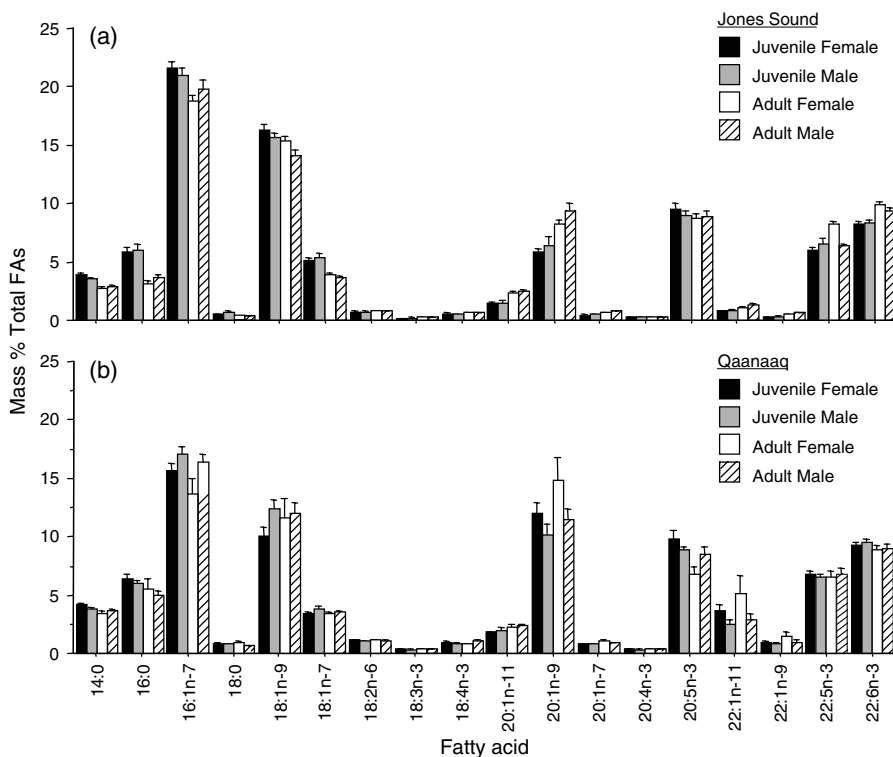


Figure 6. The 17 most abundant and variable FAs, plus 18:0 (mass % of total + 1 SEM) of ringed seals sampled in (a) Jones Sound, and (b) Qaanaaq. FA signatures in Jones Sound ringed seals differed by age (juvenile  $n = 12$ , adult  $n = 28$ ;  $P < 0.001$ ), and by sex (male  $n = 18$ , female  $n = 22$ ;  $P = 0.010$ ). Only sex had a significant effect on Qaanaaq ringed seals (Sex: male  $n = 22$ , female  $n = 20$ ;  $P < 0.001$ ; Age: juvenile  $n = 28$ , adult  $n = 14$ ;  $P = 0.197$ ).

All Qaanaaq seals were also sampled in 1998, and FA signatures differed by sex (MANOVA on 13 FAs: Wilks'  $\lambda = 0.295$ ,  $P < 0.001$ ) but not by age class (Wilks'  $\lambda = 0.577$ ,  $P = 0.197$ ; Fig. 6b). However, despite the significant overall difference between males and females, *post hoc* Bonferroni comparisons found that none of the thirteen FAs differed individually between the sexes. That is, although overall signatures differed between the genders, the differences in individual FA levels were not large enough to be statistically significant.

### *Temporal Variability*

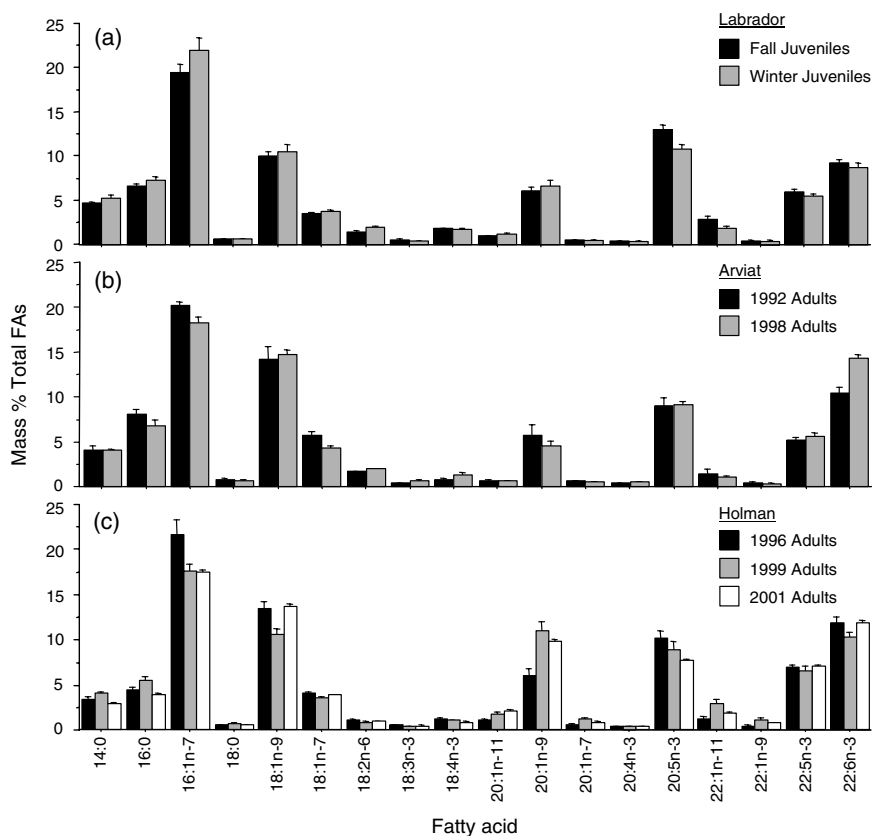
Only along the coast of Labrador were seals sampled at different seasons (Table 1), thus allowing preliminary analysis of seasonal FA trends. Juveniles sampled in the fall had significantly different FA signatures than those in winter (MANOVA on ten FAs: Wilks'  $\lambda = 0.206$ ,  $P = 0.002$ ; Fig. 7a), with fall seals having significantly less 16:0 and more 20:5n-3 and 22:1n-11. It should be noted that samples in this region were collected from 1994 to 1997, and although the seasonal distribution of samples was relatively even across years, the potential impact of interannual effects could not be assessed. The sample sizes from other regions were insufficient to adequately test for seasonal or interannual trends. However, there appeared to be some longer-term differences among adult ringed seals sampled near Arviat in 1992 ( $n = 5$ ) and 1998 ( $n = 13$ ; Fig. 7b) as well as those sampled near Holman in 1996 ( $n = 8$ ), 1999 ( $n = 10$ ), and 2001 ( $n = 21$ ; Fig. 7c).

## DISCUSSION

Iverson *et al.* (2006) demonstrated that ringed seal FA signatures can be accurately distinguished from those of other arctic pinnipeds, including bearded seals (*Erignathus barbatus*), harp seals (*Pagophilus groenlandicus*), hooded seals (*Cystophora cristata*), and walrus (*Odobenus rosmarus*); an observation that is consistent with species-specific foraging (*e.g.*, Bowen and Siniff 1999). K  kel   *et al.* (1993, 1995) and K  kel   and Hyv  rinen (1998) found differences in the FAs profiles of ringed seal subspecies inhabiting marine, brackish, and freshwater environments. Given their ubiquitous distribution across the Canadian Arctic, ringed seal FA signatures may also reflect regional differences in prey assemblages or prey FA composition. Furthermore, variability among demographic groups may occur, as has been shown for other pinnipeds (Beck *et al.* 2005). The results of our study confirm that over both large and fine scales, ringed seals exhibit significant spatial, temporal, and demographic differences in blubber FA signatures. These trends appear to be consistent with documented differences in ringed seal diets (see references below).

### *Regional Variability*

Previous studies have demonstrated that the FA composition of marine mammal blubber is largely determined by diet (*e.g.*, Ackman and Eaton 1966; Iverson 1993; K  kel   *et al.* 1993; Iverson *et al.* 1995, 2004; K  kel   and Hyv  rinen 1998; Kirsch *et al.* 2000) and that variability in FA signatures can reflect spatial differences in predator foraging (Iverson *et al.* 1997). We found that ringed seal FA signatures differed from north to south and east to west across the Canadian Arctic. FA signatures accurately reflected the location where ringed seals were sampled, and the scale of



**Figure 7.** The seventeen most abundant and variable FAs, plus 18:0 (mass % of total + 1 SEM) of (a) juvenile ringed seals off the coast of Labrador, (b) adults near Arviat, and (c) adults sampled near Holman. Labrador seals showed significant seasonal variability in FA signatures (fall  $n = 14$ , winter  $n = 11$ ;  $P = 0.002$ ). Adults sampled near Arviat in 1992 ( $n = 5$ ) and 1998 ( $n = 13$ ), and those near Holman in 1996 ( $n = 8$ ), 1999 ( $n = 10$ ), and 2001 ( $n = 21$ ) appeared to show some interannual variability. However, small sample size precluded statistical analyses of these apparent interannual differences.

FA differences tended to be related to the physical distance between groups. The consistent differences between regions that were observed whether samples were pooled across years (Fig. 3a) or limited to a single year (Fig. 3b) suggest that regional effects tend to be larger than interannual differences.

Analyses of both ringed seal FA profiles (Fig. 3a) and stomach contents (Lowry *et al.* 1980, Siegstad *et al.* 1998, Wathne *et al.* 2000, Holst *et al.* 2001) indicate large-scale regional variation in diets. Such variability is likely a consequence of the localized foraging habits of ringed seals (McLaren 1958). For instance, Born *et al.* (2004) found that ringed seals at Qaanaaq spent roughly 90% of their time in the same general area of eastern Baffin Bay. Consistent with this, discriminant analysis showed that samples from Qaanaaq overlapped only slightly with those from Jones Sound, on the opposite side of Baffin Bay (Fig. 3a). Stomach content data from each

of the seals we analyzed at Qaanaaq and Jones Sound (see Holst *et al.* 2001) showed that the diets of Qaanaaq seals were comprised primarily of arctic cod (*Boreogadus saida*) and to a lesser extent the amphipod *Themisto libellula*, whereas ringed seals in Jones Sound consumed *T. libellula*, polar cod (*Arctogadus glacialis*), and arctic cod. Therefore, in Baffin Bay, differences in ringed seal FA signatures accurately reflect spatial differences in foraging.

Given the tendency for ringed seals to forage within limited areas, the overlap in FA signatures among seals in Qaanaaq and Frobisher-Labrador (Fig. 3) suggests dietary similarities between the two areas rather than large-scale migration along the eastern coast of Canada. However, regional patterns in predator FA signatures may also be affected by regional patterns in prey FA composition. Thus, without FA data from potential prey, we are unable to quantify the dietary overlap between Frobisher-Labrador and Qaanaaq. However, three lines of evidence suggest that the patterns in FA signatures may directly reflect patterns in ringed seal foraging in these areas. First, the northward-flowing West Greenland Current, which flows west across northern Baffin Bay to join the south-flowing Baffin Bay Current, may result in some intermixing of prey in Frobisher-Labrador and Qaanaaq. Second, the limited evidence to date suggests that the diets of arctic cod throughout the Baffin Bay-Davis Strait region are dominated by copepods (Bradstreet and Cross 1982, Bradstreet *et al.* 1986). Therefore, the FA composition of available ringed seal prey may be similar in Frobisher-Labrador and Qaanaaq. Third, even if the FA signatures of ringed seal prey differ between Frobisher-Labrador and Qaanaaq, such within-species variability is likely to be substantially less than the variability between prey species (Budge *et al.* 2002). Therefore, the degree of FA overlap among seals in the eastern Canadian Arctic likely reflects dietary overlap. Given the importance of arctic cod in the diets of ringed seals near Qaanaaq (Holst *et al.* 2001), FA signatures suggest that arctic cod are also important prey for seals in Frobisher-Labrador. Earlier studies indicate that arctic cod are the dominant prey of ringed seals of northeastern Baffin Island (Bradstreet and Cross 1982, Finley *et al.* 1983) and Hudson Strait (McLaren 1958), suggesting substantial similarity, and probably preference where and when cod are available, among the diets of ringed seals throughout the eastern Canadian Arctic.

Despite the apparently broad similarity in ringed seal diets throughout the eastern Arctic, FA signatures also indicate fine-scale regional differences within the Frobisher-Labrador and Beaufort-Amundsen regions (Fig. 4). Fine-scale trends in Beaufort-Amundsen were consistent whether samples were pooled across time or limited to a single year. However, interannual effects on regional differences in Frobisher-Labrador could not be eliminated. Nonetheless, fine-scale differences in ringed seal FA profiles are consistent with previous analyses of stomach contents; although arctic cod may generally dominate diets in the eastern Arctic, *T. libellula* appears to be the primary prey of ringed seals off the eastern coast of Baffin Island (Dunbar 1941) as well as those inhabiting the offshore pack ice in northern Baffin Bay (Finley *et al.* 1983). Lowry *et al.* (1980) found that ringed seal diets differed between the western and central Beaufort Sea and between samples from the northeastern and north-central Bering Sea. Although the specific dietary differences between Frobisher Bay and Labrador seals, or between Banks Island and Holman seals, are unknown, FA signature analysis has previously detected foraging differences among seals separated by as little as 9–15 km (Iverson *et al.* 1997).

Consistent with the relatively isolated and inland location of Hudson Bay, and the influence of large amounts of inflowing fresh water, seals sampled at Arviat and the Belcher Islands had more distinctive FA signatures than those from other

parts of the Arctic. Although relatively little is known about the specific foraging habits of ringed seals in Hudson Bay, our data suggest that individuals in the northwestern and southeastern areas of the bay have different diets. Differences in the timing and distribution of annual ice and open water, as well as the inflow of fresh water in different parts of the bay, may result in differences in prey distribution between the two Hudson Bay regions. It should also be noted that ringed seals were sampled earlier at Arviat (1992 and 1998) than the Belcher Islands (2003), so the possibility of a long-term shift in the available prey in Hudson Bay cannot be discounted. For instance, between the mid-1980s and late 1990s, Gaston *et al.* (2003) observed a significant decline in the proportion of arctic cod and an increase in capelin (*Mallotus villosus*) and sandlance (*Ammodytes* spp.) in the food delivered to nestling thick-billed murres (*Uria lomvia*) in northern Hudson Bay. They attributed the shift to long-term climate warming that increased the amount of open water near the murre colony (Moritz *et al.* 2002, Gagnon and Gough 2005) and changed the availability (and likely the abundance) of the fish species involved. Given that large-scale climatic shifts (Stirling *et al.* 1999, Gough *et al.* 2004, Gagnon and Gough 2005) appear to be having negative effects on ringed seal recruitment in Hudson Bay (Ferguson *et al.* 2005, Stirling 2005), it is possible that ringed seal diets may also be changing.

#### *Demographic Variability*

Sex- and age-related differences in ringed seal FA signatures were highly variable across regions. Seals in Frobisher-Labrador, Jones Sound, and Qaanaaq showed some demographic variability, whereas those in Beaufort-Amundsen and Arviat did not. These inconsistent trends are similar to the variability seen in other studies of ringed seal foraging. McLaren (1958) found no age- or sex-specific differences in ringed seal diets in southwestern Baffin Island or northern Foxe Basin. Kenyon (1962), Lowry *et al.* (1978), and Siegstad *et al.* (1998) also reported no demographic variability in the stomach contents of ringed seals from western Alaska, northern Alaska, and northwestern Greenland, respectively. In contrast, Lowry *et al.* (1980) found that saffron cod (*Eleginus gracilis*) were eaten in greater quantities by adult ringed seals in the Bering Sea than by juveniles, but that age-related differences in diet were less dramatic or non-existent in the Chukchi and Beaufort Seas.

The FA signatures of ringed seals in Frobisher-Labrador differed by age (Fig. 4), with young-of-the-year (YOY) and adults appearing most similar (Fig. 5). This adult-YOY similarity may be a consequence of direct transfer of maternal FAs to the nursing pup *via* milk (see Iverson *et al.* 1995). There were also age-specific differences in FA signatures in Jones Sound, where stomach content data (Holst *et al.* 2001) revealed that adult ringed seal diets were dominated by polar cod, whereas juveniles fed primarily on *T. libellula*. These trends may be related to the spatial segregation of ringed seals by age, as subadults are often excluded from preferred fast-ice habitats and forced to forage farther offshore (McLaren 1958, Stirling 1977). Adult ringed seals may also forage at greater depths (Born *et al.* 2004) where polar cod can be abundant (Cohen *et al.* 1990). At Qaanaaq, where ringed seal diets were dominated by arctic cod, there were no age-related differences in stomach contents (Holst *et al.* 2001) or FA signatures. This supports the hypothesis of Lowry *et al.* (1980) that arctic cod are caught as easily by ringed seal pups as by adults and that age-related differences tend to be absent where arctic cod are the dominant prey.



FA signatures indicated sex-specific foraging patterns among ringed seals in both Jones Sound and Qaanaaq. Although Holst *et al.* (2001) found no differences in the stomach contents of male and female ringed seals in either area, their stable isotope analyses indicated a significant sex effect among Qaanaaq seals. Collectively, these observations suggest that stable isotope and FA analyses, both of which provide an indication of longer-term dietary intake, may reveal foraging differences that are not apparent in the “snapshot” data provided by stomach contents.

### *Temporal Variability*

The FA signatures of juvenile ringed seals sampled in the fall and winter off Labrador suggested significant seasonal changes in foraging patterns (Fig. 7a). Previous analyses of stomach contents have indicated no seasonality in ringed seal diets in nearby Hudson Strait, northern Foxe Basin, or western Beaufort Sea (McLaren 1958, Lowry *et al.* 1978). Conversely, Weslawski *et al.* (1994) and Siegstad *et al.* (1998) observed seasonal shifts in the diets of ringed seals near Svalbard and off western Greenland, respectively. Lowry *et al.* (1980) presented compelling evidence that seals in the Bering Strait, southeastern Chukchi Sea, and central Beaufort Sea feed primarily on arctic cod during winter months when the fish concentrate near the shore to breed but shift to a diet of pelagic crustaceans during summer months when the cod disperse into deeper water. Smith (1987) observed the same seasonal trend among ringed seals in Amundsen Gulf. A fall-to-winter increase in arctic cod consumption may account for the seasonal change in FA signatures we observed in ringed seals off Labrador.

We did not have adequate sample sizes from any one age group, season, and geographic region to statistically test for interannual variability in ringed seal FA signatures. However, the limited number of samples we had from adults in Arviat (Fig. 7b) and Beaufort-Amundsen (Fig. 7c) suggest that there may be year-to-year changes in ringed seal diets. Considering the opportunistic nature of ringed seal foraging (McLaren 1958), some interannual variability should be expected as particular prey species undergo natural fluctuations in abundance. The FA signatures of ringed seal prey should be relatively stable across years (Iverson *et al.* 2002), especially when compared to differences between prey species. Therefore, systematic collection of ringed seal FA data over extended time scales could be used to identify long-term changes in ringed seal diets and to separate these trends from year-to-year variability. This, in turn, could reflect food web responses to long-term environmental change, including climate warming.

Our results demonstrate that the FA signatures of ringed seals vary over both coarse and fine spatial scales and suggest trophic relationships that are consistent with stomach content and stable isotope analyses. In agreement with previous studies, FA signatures indicate broad similarities in the diets of ringed seals in the eastern Arctic; however, fine-scale differences also exist in some areas. Age and sex appear to have variable effects on ringed seal foraging, and their influence likely depends on the prey assemblage in a given area. As would be expected for an opportunistic forager in a dynamic environment, ringed seals may vary their diets seasonally as well as over longer periods. We suggest that further systematic collection of blubber samples, both at a variety of locations and throughout the year, could provide crucial insights into the long-term effects of environmental change on arctic food webs.

## ACKNOWLEDGMENTS

We are particularly grateful to the native hunters of Nunavut and Newfoundland and Labrador for collecting fat samples from ringed seals harvested in their subsistence hunts. Thanks also to G. Gilchrist (Canadian Wildlife Service, Ottawa), L. Harwood (Fisheries and Oceans Canada, Yellowknife), D. Muir (National Water Research Institute), J. Palm, J. Beauchesne, and F. Piugattuk (Nunavut Department of Sustainable Development), B. Sjare (Fisheries and Oceans Canada, St. John's), and C. Sonne-Hansen (Greenland Ministry of Environment) for collecting and sharing specimens, and to S. Lang for invaluable assistance in the lab. A. Pabst and three anonymous reviewers provided valuable comments on an earlier version of the manuscript. This study was primarily supported by Natural Sciences and Engineering Research Council (NSERC, Canada) and Killam Trust Scholarships to G.W.T., by NSERC operating and equipment grants to S.J.I., and by the Canadian Wildlife Service. We are also grateful to the following organizations for additional financial support: the Northern Scientific Training Program, Dr. Patrick Lett Fund, Government of Northwest Territories, Government of Nunavut, National Fish and Wildlife Foundation, Nunavut Wildlife Management Board, World Wildlife Fund (Canada and International), Polar Continental Shelf Project, Fisheries and Oceans Canada, and the Churchill Northern Studies Centre.

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Received: 24 March 2006

Accepted: 6 September 2006