

# Intrinsic and extrinsic sources of variation in the diets of harp and hooded seals revealed by fatty acid profiles

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**Abstract:** Individuals of different age, sex, and morphology are expected to exhibit differences in dietary niches largely owing to sexual dimorphism, ontogenetic niche shifts, and resource polymorphism. Harp (*Pagophilus groenlandicus* (Erxleben, 1777)) and hooded (*Cystophora cristata* (Erxleben, 1777)) seals are geographically overlapping and highly migratory predators in the North Atlantic Ocean. These species differ in their diving behaviour, with hooded seals diving deeper, longer, and more associated with the continental shelf edge and deep ocean than harp seals. We examined blubber fatty acid (FA) composition ( $N = 37$ ; 93% of total FA by mass) of harp (adults  $N = 294$ ; juveniles  $N = 232$ ) and hooded (adults  $N = 118$ ; juveniles  $N = 38$ ) seals to test hypotheses about sources of intrinsic (age and sex) and extrinsic (geographic location, season, year) variations in diets. A significant difference in FA profiles suggested dietary segregation between species. We found significant effects of sex and age class on FA profiles, with these being more pronounced in the highly size-dimorphic hooded seals than in harp seals. FA profiles of both species also varied between inshore and offshore sampling locations and between prebreeding and postbreeding periods. Finally, FA profiles of harp seals differed among years, which was coincident with large changes in prey distribution and availability in the mid-1990s.

**Résumé :** On s'attend à ce que des individus différents par l'âge, le sexe ou la morphologie possèdent aussi des différences de niche alimentaire principalement à cause du dimorphisme sexuel, des changements ontogéniques de niche et du polymorphisme des ressources. Les phoques du Groenland (*Pagophilus groenlandicus* (Erxleben, 1777)) et les phoques à capuchon (*Cystophora cristata* (Erxleben, 1777)) sont des prédateurs fortement migrants de l'Atlantique Nord dont les aires de répartition géographique se chevauchent. Ces espèces diffèrent dans leur comportement de plongée, les phoques à capuchon faisant des plongées plus profondes, plus longues et plus fortement associées au bord du plateau continental et à l'océan profond que les phoques du Groenland. Nous avons analysé la composition en acides gras (FA) du lard ( $N = 37$ ; 93 % en masse des FA totaux) de phoques du Groenland ( $N = 294$ ; jeunes  $N = 232$ ) et de phoques à capuchon ( $N = 118$ ; jeunes  $N = 38$ ) afin de tester des hypothèses sur les sources intrinsèques (âge et sexe) et extrinsèques (position géographique, saison, année) de variation du régime alimentaire. Une différence significative entre les profils de FA laisse croire à une ségrégation alimentaire entre les deux espèces. Il existe des effets significatifs du sexe et de la classe d'âge sur les profils de FA qui sont plus prononcés chez le phoque à capuchon qui affiche un fort dimorphisme de la taille que chez le phoque du Groenland. Les profils de FA des deux espèces diffèrent aussi entre les sites d'échantillonnage du bord et du large, ainsi que durant les périodes avant et après la reproduction. Enfin, les profils de FA du phoque du Groenland varient entre les années, ce qui coïncide avec les importants changements dans la répartition et la disponibilité des proies qui se sont produits au milieu des années 1990.

[Traduit par la Rédaction]

## Introduction

Diet has important consequences for gross energy intake, foraging costs, and exposure to foraging-specific risk factors such as predation and competition (Bolnick et al. 2003). Interspecific competition for prey has been viewed traditionally as a fundamental mechanism structuring ecological communities and the niche breadth of individual species

(Pianka 1981; Polis 1984). Increasingly, intraspecific competition also has been identified as a significant mechanism in the evolution of niche breadth (Polis 1984; Williams and Martinez 2000; Bolnick et al. 2003). Both inter- and intra-species competition can be mitigated through resource partitioning over varying spatial and temporal scales (e.g., Kato et al. 2000; Wikelski and Wrege 2000; Bradshaw et al. 2003; Field et al. 2005). Within species, diets often diverge

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as a function of body size, age, sex, condition, and reproductive status (e.g., Clarke et al. 1998). For marine predators, differences in and the factors influencing diet are not well understood given the difficulty of making observations in this realm (Bowen et al. 2002). However, there is mounting evidence for sex differences and ontogenetic shifts in foraging behaviour and diet of size-dimorphic phocids (e.g., Le Boeuf et al. 1993, 2000; Beck et al. 2003a, 2003b, 2007; Field et al. 2005; Tucker et al. 2007).

Various hypotheses have been proposed to explain variation in diet such as niche divergence, where competition is minimized between males and females by the selection of different prey or by spatial or temporal segregation in feeding. Alternatively, but not exclusively, variable sex-specific costs of reproduction may result in differential resource use (Ginnett and Demment 1997). Also, differences in diet could simply be due to different energetic costs associated with body size (e.g., Barbosa et al. 2000) owing to either age and growth, or size dimorphism. Greater absolute energy requirements of larger animals may require differential use of resources that can result in segregation in foraging. These hypotheses could also be invoked to explain diet differences between closely related and (or) sympatric species as well.

Harp (*Pagophilus groenlandicus* (Erxleben, 1777)) and hooded (*Cystophora cristata* (Erxleben, 1777)) seals are abundant, wide-ranging, and highly migratory pinnipeds inhabiting the North Atlantic Ocean (Folkow et al. 1996; Stenson and Sjare 1997). These species partition foraging ranges and pupping habitats, and also exhibit differences in body size, degree of sexual body-size dimorphism, diving behaviour, migratory routes, and the time and energy invested in reproduction (Lydersen and Kovacs 1999). Harp seals are only slightly dimorphic, with males being 5% heavier than females and having a mean adult mass of 130 kg (Hammill et al. 1995). Hooded seals exhibit greater size dimorphism, with adult males 1.5 times heavier than hooded females, and 2.3 times heavier than adult harp seals (Hammill and Stenson 2000). Harp seals mainly inhabit the continental shelf (Stenson and Sjare 1997; Folkow et al. 2004), whereas hooded seals are more associated with the continental shelf edge and deep ocean (Folkow and Blix 1999; G.B. Stenson, unpublished data). Most harp seal dives are <50 m, although dives to 200 m (Stenson and Sjare 1997; Folkow et al. 2004) have been recorded, whereas hooded seals regularly dive to depths >300 m and often exceed 1000 m (Folkow and Blix 1999; G.B. Stenson, unpublished data). Harp seals segregate foraging range by sex and age class (Sergeant 1965, 1991). In contrast to sex differences in diving behaviour found in other size-dimorphic pinnipeds (Le Boeuf et al. 1993, 2000; Beck et al. 2003a, 2003b; Field et al. 2005; Breed et al. 2006), Folkow and Blix (1999) found no individual-, sex-, or size-related differences in dive parameters for mature hooded seals, although sample size was small.

Relatively few studies have documented diets for harp and hooded seals across their entire range given that these animals are far-ranging and large portions of the population are essentially inaccessible to researchers for most of the year. Thus, diet estimates are often biased by nearshore sampling during particular times of the year. Information to date is based mostly on conventional stomach-content analysis with samples collected in different locations, seasons, and

years, and has often suffered from small sample sizes across age classes. Moreover, there are well-known analytical limitations associated with stomach-content analysis (Jobling and Breiby 1986; Jobling 1987) that may further bias our estimation of what these seals consume. These include differential rates of digestion, the lack of diagnostic hard parts of some soft-bodied prey, and the fact that these assessments provide only a snapshot of the most recent meal and may not be representative of the longer term diet. Species differences in diving patterns of these two ice-breeding species are generally reflected in the average diets estimated from stomach-content analyses. Data indicate that harp seals consume a mixed diet of capelin (*Mallotus villosus* (Müller, 1776)), Arctic cod (*Boreogadus saida* (Lepechin, 1774)), and herring (*Clupea harengus* L., 1758), as well as many other fish species, and invertebrates such as euphausiids (Lawson and Stenson 1995, 1997; Lawson et al. 1995). Diets of hooded seals are poorly studied, but they are presumed to feed mostly on deepwater fish such as Atlantic halibut (*Hippoglossus hippoglossus* (L., 1758)), redfish (genus *Sebastes* Cuvier, 1829), and the squid *Gonatus fabricii* (Lichtenstein, 1818), as well as capelin, Atlantic cod (*Gadus morhua* L., 1758), and Arctic cod (Ross 1993; Kapel 1995; Hammill and Stenson 2000; Potelov et al. 2000; Haug et al. 2007). Despite the paucity of data and potential biases associated with this analysis, available data suggest inter- and intra-specific variations in diets with additional geographical, annual, and seasonal effects (e.g., Lawson and Stenson 1995, 1997; Lawson et al. 1995, 1998) warranting further exploration given the perceived importance of these predators in the North Atlantic ecosystem.

Limitations of stomach-content analysis have led to the development of alternative biochemical methods for estimating diets of predators. For several species of marine mammals, seabirds, and terrestrial carnivores, analysis of fatty acids (FAs) stored in adipose tissue depots has provided an assessment of temporal or spatial differences in diet (e.g., Smith et al. 1996, 1997; Iverson et al. 1997; Beck et al. 2005) and a quantitative estimate of the species composition of the diet (Iverson et al. 2004; Beck et al. 2007; Iverson et al. 2007). Because FAs are deposited in predator adipose tissue in a predictable manner and there are limits on FA biosynthesis in higher order consumers, many FAs found in pinniped blubber can be attributed largely or solely to dietary sources (Iverson 1993, 2009). We refer to the entire suite of blubber FAs as an individual's FA profile. Blubber FAs represent an integration of the dietary intake of individuals over periods of weeks or months (Iverson et al. 2004; Budge et al. 2006) so that sampling locations of wide-ranging species are less likely to bias our understanding of dietary differences than stomach contents, which represent only recent feeding. Thus, differences in consumer FA profiles represent differences in diets (Iverson et al. 1997; Smith et al. 1997; Beck et al. 2005; Budge et al. 2006) and provide a useful tool for examining sources of variation in diet over ecologically meaningful time scales (i.e., those affecting growth and survival).

In this study, we analyzed blubber FA profiles to examine several sources of variation in the diets of harp and hooded seals. Given their broad geographic distribution and pronounced seasonal migrations, we expected to find differen-

ces in the diet over time and space. However, to date most samples have been collected in winter from relatively near-shore locations or at times when stomachs are empty, providing little opportunity for testing this expectation. Large changes in fish assemblages of the North Atlantic with the collapse of groundfish stocks in the early 1990s (e.g., Hutchings and Myers 1994; Rose 2004) and the coincidental changes in the abundance and distribution of pelagic forage fish (Frank et al. 1996; Carscadden et al. 2001) and seals (Lacoste and Stenson 2000; Hammill and Stenson 2000) provided the opportunity to examine how these species responded to such interannual changes in their prey. Harp seals exhibit little body-size dimorphism, but hooded seals exhibit a degree of sexual size dimorphism that, in other species (i.e., grey seal (*Halichoerus grypus* (Fabricius, 1791)); Beck et al. 2005), is associated with sex-specific differences in diet. Therefore, we expected sex differences in diet reflected in FA profiles in hooded seals but not in harp seals. Finally, given that ontogenetic differences in diet are evident in harp seals (stomach contents; Lawson and Stenson 1995) and other pinniped species, we tested for age effects on FA profiles. Overall, we tested for the effects of two intrinsic factors (age class and sex) and three extrinsic factors (season, year, and geographic sampling location).

## Materials and methods

### Sampling

Blubber samples were obtained from harp and hooded seals killed under permit along the northeast coast of Newfoundland and southern Labrador between November and May from 1994 to 2004 by experienced seals hunters and scientific personnel from Fisheries and Oceans Canada, formerly Department of Fisheries and Oceans (Sjare et al. 2004) (Fig. 1; Tables 1, 2). Evidence from grey seals (Cooper 2004) suggests that blubber lipid composition in phocid seals is uniform throughout the main trunk of the body (i.e., dorsal, ventral, lateral, anterior, and posterior). Nevertheless, for consistency we took samples from the same location in all animals. A full-depth blubber sample (approximately 0.5 kg from skin to underlying muscle) was taken from the posterior mid-flank (where blubber and fat storage is thickest) of each seal, and placed in a Whirlpak<sup>®</sup> and frozen. The age of seals was determined to the nearest year by sectioning a lower canine tooth and counting dentine cementum annuli (Bowen et al. 1981). In addition to the samples from killed seals, full-depth biopsy samples were taken from the posterior mid-flank of seals live-captured during an offshore cruise to the whelping patch on the pack ice off southern Labrador (the “Front”) in March 2004 (31 harp and 12 hooded seals) and to the moulting patch off eastern Greenland in June 2005 (17 hooded seals). All procedures used in this study were in accordance with the principles and guidelines of the Canadian Council on Animal Care adopted by Fisheries and Oceans Canada. A map of sampling locations was generated using an R-based (R<sup>®</sup> version 2.6.2; R Development Core Team 2008) package (PBS mapping version 2.55; Schnute et al. 2008).

Harp seal juveniles (1–4 years) and adults (5+ years) (Sjare et al. 2004) were grouped by season: prebreeding (November–March) and postbreeding (April–May), and year

(Table 2). No harp seals were sampled during the summer. Seals were also grouped by sampling location: inshore (defined as <30 km from shore) and offshore (defined as >30 km from shore) (Lawson et al. 1995). Offshore areas are typically over water depths exceeding 200 m (see Fig. 1). Hooded seal juveniles (1–5 years) and adults (6+ years) were also grouped into pre- and post-breeding periods (where breeding occurred in mid-March) and sampling area (inshore and offshore as defined above, and Greenland).

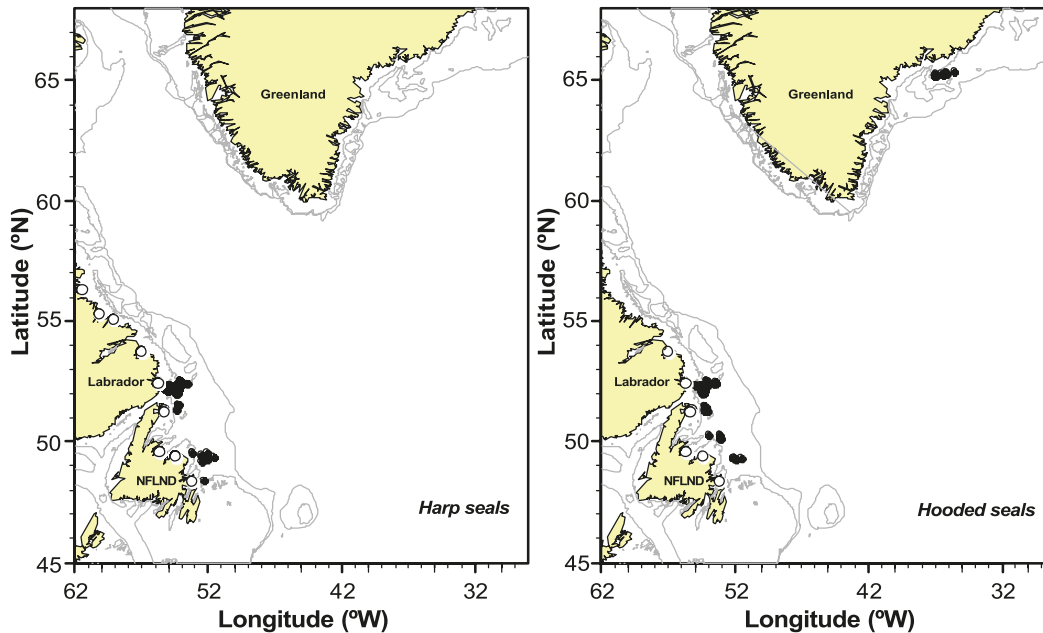
### Fatty acid analysis

To obtain equivalent samples from all seals, in the laboratory a 0.5 g full-depth core of blubber was taken from the larger sample collected in the field from the killed seals. Lipids were quantitatively extracted from all blubber samples using a modified Folch method (Folch et al. 1957; Iverson et al. 2001) and FA methyl esters (FAME) were prepared using an acidic catalyst (the Hilditch method; see Iverson et al. 2001; Budge et al. 2006). Duplicate analyses and identification of FAME were performed using temperature-programmed gas–liquid chromatography (GLC) (Iverson et al. 1997, 2004; Budge et al. 2006). FAs were described 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. Individual FAs were expressed as a percent mass of total FAs. Although 67 FAs are routinely identified, we used 39 FAs of dietary or primarily dietary origin (Iverson et al. 2004; Beck et al. 2005; Budge et al. 2006), which accounted for approximately 93% of total FA by mass. Dietary FAs are unmodified FAs that are directly deposited in adipose tissue, whereas primarily dietary FAs are FAs that are modified at some point between absorption and deposition but whose levels in a predator are highly influenced by consumption of specific prey. Proportional data were normalized using a natural logarithmic transformation according to the following equation:  $x_{\text{trans}} = \ln(x_i/c_r)$ , where  $x_{\text{trans}}$  is the transformed data,  $x_i$  is a FA expressed as percentage of total FAs, and  $c_r$  is the percentage of a reference FA, in this case 18:0 (Budge et al. 2002).

### Statistical analysis

Multivariate analysis of variance (MANOVA) and discriminant function analysis (DFA) were used to investigate the effects of species, sex, age class, sampling area, season, and in the case of harp seals, year on FA profiles (SPSS<sup>®</sup> version 11.5; SPSS Inc. 2002). In MANOVA (using type III sum of squares), significance of combined dependent variables (i.e., FAs) on predictor variables was assessed using Wilks'  $\lambda$ . Strength of the association of the combined dependent variables and the predictor variables was assessed by partial  $\eta^2$  ( $\eta^2_{\text{partial}} = 1 - \text{Wilks' } \lambda$  when  $s = 1$  and  $\eta^2_{\text{partial}} = 1 - (\text{Wilks' } \lambda)^{1/s}$  when  $s > 1$ ; Tabachnick and Fidell 2001), where larger values indicate a greater amount of variation accounted for by the model effect. All two-way interactions were also evaluated for significance in all MANOVAs; however, we report only the significant interaction terms. The same FA sets were used in DFA. DFA was used to illustrate the relative difference in FA profiles between main effects by plotting the first two DFA scores, which typically accounted for >85% of the variance in FA profiles. Because

**Fig. 1.** Map of sampling locations for harp (*Pagophilus groenlandicus*;  $n = 526$ ) and hooded (*Cystophora cristata*;  $n = 156$ ) seals (1994–2005). Open circles denote inshore areas and solid circles denote offshore sampling locations. Lines represent the 200, 500, and 2500 m isobaths.



**Table 1.** Sample sizes of juvenile, adult female, and adult male harp (*Pagophilus groenlandicus*) and hooded (*Cystophora cristata*) seals from prebreeding and postbreeding periods and different locations.

Species	Age class	Prebreeding			Postbreeding		
		Inshore	Offshore	Biopsy samples	Inshore	Offshore	Biopsy samples
Harp	Juvenile	144	41	—	11	36	—
	Adult female	97	25	31	11	25	—
	Adult male	47	39	—	8	11	—
Hooded	Juvenile	31	2	—	—	2	3
	Adult female	17	11	8	3	7	9
	Adult male	27	13	2	3	10	5

**Note:** Blubber biopsy samples from live-captured animals in the prebreeding period were taken from the “Front”, while biopsy samples in the postbreeding period were taken from East Greenland.

**Table 2.** Sample sizes of juvenile, adult female, and adult male harp seals (*Pagophilus groenlandicus*) from individual years (1994–2004).

Age class	Year						
	1994	1995	1996	1998	2000	2002	2004
Juvenile	20	30	48	20	16	33	65
Adult female	11	12	23	24	11	40	37
Adult male	23	6	12	15	5	14	30

**Note:** Samples are pooled across seasons and sampling locations.

the sample size of any group must exceed the number of response variables tested by MANOVA or DFA (Stevens 1986), smaller subsets of FAs (outlined below) were used in some analyses. In these cases, we selected those FAs that exhibited the greatest mean variances across samples to maximize the amount of information retained. Homogeneity of variance across and between groups was evaluated with Box’s M and Levene’s tests, respectively.

First, we compared FA profiles between species by pooling all harp and hooded seals. We used the entire 39 FA set, with species, sex, age class, and season as main effects in

MANOVA. Next, we tested for intrinsic (sex and age class) and extrinsic (season, sampling area, and year in the case of harp seals) effects within each species. For harp seals, we used 31 FAs, which accounted for 92% of total FAs by mass. Adults that were biopsied from the whelping patch were dropped from this analysis, as we had no knowledge of where they might have fed prior to giving birth. To test for intrinsic and seasonal effects on FA profiles of hooded seals, we first used a subset of 37 FAs (92.5% of total FAs) in a separate MANOVA. Because sample size varied greatly among sampling locations, we constructed a second MAN-

OVA using a smaller subset of 17 FAs (89% of total FAs), which also included sampling location as a main effect.

## Results

Over the 10-year period, blubber samples were obtained from 526 harp seals and 153 hooded seals (Table 1). Roughly equal numbers of males and females were sampled at each time period. The mean FA compositions of each species and age class are shown in Table 3. Combining both species, seven FAs (16:0, 16:1*n*-7, 18:1*n*-9, 20:1*n*-9, 20:5*n*-3, 22:1*n*-11, and 22:6*n*-3), each >5% of total FAs by mass, accounted for approximately 68% of the total FAs. Saturated, monounsaturated, and polyunsaturated FAs accounted for 15.9%, 56.8%, and 27.3%, on average, of total FAs by mass, respectively (Table 3).

### Species differences

We found a significant effect of species (MANOVA: Wilks'  $\lambda$   $F_{[38,631]} = 56.32$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.77$ ), age class (Wilks'  $\lambda$   $F_{[38,631]} = 9.55$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.37$ ), season (Wilks'  $\lambda$   $F_{[76,631]} = 6.86$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.29$ ), sampling area (Wilks'  $\lambda$   $F_{[76,1262]} = 4.67$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.22$ ), and sex (Wilks'  $\lambda$   $F_{[38,631]} = 2.94$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.15$ ) on blubber FA profiles. Harp and hooded seals differed significantly in percentages of 36 of the 39 FAs (MANOVA, test of between-subject effects:  $P < 0.05$  in all cases). Differences were most pronounced in the levels of 22:5*n*-3, 22:6*n*-3, and 21:5*n*-3, which were all higher in harp seals (Table 3). Interaction terms between species and all other variables were also significant, indicating that the effects of each of these independent variables on FA profiles differed between harp and hooded seals: sex (Wilks'  $\lambda$   $F_{[38,631]} = 3.05$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.16$ ), age class (Wilks'  $\lambda$   $F_{[38,631]} = 4.21$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.20$ ), season (Wilks'  $\lambda$   $F_{[38,631]} = 5.40$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.25$ ), and sampling area (Wilks'  $\lambda$   $F_{[38,631]} = 2.40$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.13$ ).

Differences in the FA profiles of harp and hooded seals and of age groups within species are illustrated in Fig. 2. Species differed along the first discriminant function (91.3% of the variance in FA profiles), while age classes differed along the second discriminant function (6.8% of the variance). Overall, 83.4% of the grouped cases were correctly classified to species. All misclassifications were between age classes (within each species) and not owing to misclassifications between species.

### Harp seals

We found a significant effect of age class (MANOVA: Wilks'  $\lambda$   $F_{[30,445]} = 4.89$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.25$ ), sex (Wilks'  $\lambda$   $F_{[30,445]} = 2.54$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.15$ ), season (Wilks'  $\lambda$   $F_{[30,445]} = 8.14$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.35$ ), sampling location (Wilks'  $\lambda$   $F_{[30,445]} = 1.63$ ,  $P = 0.021$ ,  $\eta^2_{\text{partial}} = 0.10$ ), and year (Wilks'  $\lambda$   $F_{[180,2633]} = 6.35$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.30$ ) on harp seal FA profiles. There were significant interactions between age class and season (Wilks'  $\lambda$   $F_{[30,445]} = 1.74$ ,  $P = 0.010$ ,  $\eta^2_{\text{partial}} = 0.11$ ) and between age class and year (Wilks'  $\lambda$   $F_{[30,2700]} = 2.26$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.13$ ), indicating that the way juvenile and adult diets changed differed at these two temporal scales. Adult and juvenile harp seals differed significantly in 20 of 31 FAs

(MANOVA, test of between-subject effects:  $P < 0.05$  in all cases). Differences were most pronounced in the levels of 22:1*n*-7 and 22:1*n*-9, which were higher in adults. There were also significant interactions between sampling location and season (Wilks'  $\lambda$   $F_{[30,445]} = 1.70$ ,  $P = 0.013$ ,  $\eta^2_{\text{partial}} = 0.10$ ) and between sampling location and year (Wilks'  $\lambda$   $F_{[60,890]} = 2.37$ ,  $P < 0.001$ ,  $\eta^2_{\text{partial}} = 0.14$ ), suggesting again that FA profiles of inshore and offshore animals did not change in the same manner at these temporal scales. We then ran separate MANOVAs for juveniles and adults. This revealed that there was no effect of sex on juvenile FA profiles (Wilks'  $\lambda$   $F_{[30,199]} = 1.48$ ,  $P = 0.06$ ), but there was a sex effect in adults (Wilks'  $\lambda$   $F_{[30,222]} = 2.07$ ,  $P = 0.002$ ,  $\eta^2_{\text{partial}} = 0.22$ ). Adult males and females differed significantly in only 8 of the 31 FAs (MANOVA, test of between-subject effects:  $P < 0.05$  in all cases). Differences were most pronounced in the levels of 20:1*n*-11 and 22:1*n*-11, which were higher in males.

We used DFA to visualize the relative effect of intrinsic differences on FA profiles of harp seals. Although adults and juveniles differed significantly in their FA profiles (Fig. 2), only 69.4% of seals were correctly classified by age class. The first discriminant function (83.6% of variance in FAs) separated juveniles from adults, while the second discriminant function (16.4% of variance in FAs) separated adult males from adult females. Most misclassified cases were between adult males and females.

We then conducted separate DFA for adults and juveniles (to control for age-class differences) to illustrate the relative effects of season and sampling location. FA profiles varied seasonally in both the inshore and offshore (Fig. 3). The first discriminant function (69.4% variation in FAs) separated prebreeding samples from postbreeding offshore samples. The second function (23% variation in FAs) separated prebreeding inshore and offshore samples. Overall, 81% of individuals were correctly classified to season. Most misclassified cases were between offshore areas, as diets were more similar in the offshore and varied seasonally to a greater extent in the inshore. Similarly, in juveniles (Fig. 3) the first discriminant function (62.1% variation in FAs) separated prebreeding samples from postbreeding samples, while the second function (33.5% variation in FAs) separated prebreeding inshore and offshore samples. Overall, 78% of juveniles were correctly classified to season.

To examine sex differences in adults by season, we pooled inshore and offshore animals to increase the number of samples, because a much higher proportion of the variation in FA profiles was attributed to seasonal rather than to location effects in the previous DFA. The first discriminant function (80.2% variation in FAs) separated post- and prebreeding animals, while the second function (16% variation in FAs) separated males from females (Fig. 4). Misclassifications were primarily between sexes (25%) rather than seasons (<7%). The difference between males and females was more pronounced in the prebreeding period than in the postbreeding period, although differences were small.

During the prebreeding period, 70.8% of juveniles were correctly classified to year (Fig. 5). The first discriminant function (65.7% variation in FAs) separated 1994 from 1995 and other years, which formed a cluster. The second function (13.9% variation in FAs) separated 1994 and 1995. Similarly, in adult harp seals 74% of samples were correctly

**Table 3.** Mean (SE) fatty acid (FA; %) profiles for age classes of harp (*Pagophilus groenlandicus*) and hooded (*Cystophora cristata*) seals.

	Harp seals			Hooded seals		
	Juvenile ( <i>n</i> = 232)	Adult		Juvenile ( <i>n</i> = 35)	Adult	
		Female ( <i>n</i> = 189)	Male ( <i>n</i> = 105)		Female ( <i>n</i> = 56)	Male ( <i>n</i> = 62)
<b>Unsaturated FAs</b>						
<b>14:0</b>	5.67±0.06	5.32±0.06	5.37±0.08	5.39±0.1	4.7±0.1	4.58±0.11
16:0	8.9±0.11	8.37±0.13	8.12±0.18	10.6±0.26	8.97±0.22	8.7±0.21
<b>17:0</b>	0.16±0.004	0.14±0.01	0.11±0.01	0.19±0.01	0.17±0.01	0.15±0.01
<b>18:0</b>	1.34±0.02	1.27±0.03	1.21±0.03	1.72±0.06	1.62±0.05	1.72±0.05
<b>Monounsaturated FAs</b>						
<b>16:1<i>n</i>-7</b>	12.44±0.2	13.7±0.23	13.67±0.25	12.29±0.35	10.73±0.24	11.94±0.25
<b>18:1<i>n</i>-9</b>	14.09±0.19	12.8±0.22	11.41±0.34	19.08±0.66	20.97±0.56	20.02±0.49
<b>18:1<i>n</i>-7</b>	3.51±0.06	3.89±0.08	3.55±0.09	3.68±0.11	4.15±0.08	4.48±0.08
18:1 <i>n</i> -5	0.56±0.01	0.55±0.01	0.55±0.01	0.48±0.01	0.46±0.01	0.52±0.01
20:1 <i>n</i> -11	1.92±0.04	1.85±0.05	2.08±0.1	2.02±0.08	2.48±0.08	2.34±0.08
20:1 <i>n</i> -9	11.31±0.21	12.92±0.28	15.02±0.41	10.82±0.3	13.7±0.38	14.05±0.28
20:1 <i>n</i> -7	0.63±0.02	0.83±0.02	1.09±0.07	0.53±0.03	0.71±0.04	0.93±0.03
22:1 <i>n</i> -11	5.91±0.18	6.69±0.22	8.85±0.33	5.67±0.38	7.03±0.34	6.78±0.24
22:1 <i>n</i> -9	0.83±0.02	1.11±0.03	1.5±0.07	0.82±0.05	1.25±0.06	1.28±0.04
22:1 <i>n</i> -7	0.11±0.005	0.15±0.01	0.22±0.01	0.1±0.01	0.14±0.01	0.15±0.01
<b>Polyunsaturated FAs</b>						
16:2 <i>n</i> -6	0.08±0.01	0.07±0.002	0.081±0.01	0.22±0.01	0.19±0.004	0.23±0.01
16:2 <i>n</i> -4	0.26±0.01	0.24±0.01	0.17±0.01	0.37±0.02	0.35±0.01	0.35±0.01
16:3 <i>n</i> -6	0.5±0.01	0.54±0.01	0.64±0.02	0.18±0.01	0.17±0.01	0.19±0.01
16:3 <i>n</i> -4	0.28±0.01	0.33±0.01	0.37±0.01	0.32±0.03	0.28±0.02	0.26±0.02
16:4 <i>n</i> -1	0.48±0.01	0.59±0.02	0.64±0.03	1.5±0.03	1.51±0.03	1.46±0.03
18:2 <i>n</i> -6	1.49±0.02	1.4±0.03	1.2±0.03	0.09±0.004	0.09±0.003	0.11±0.002
18:2 <i>n</i> -4	0.11±0.002	0.11±0.002	0.11±0.002	0.12±0.003	0.11±0.003	0.12±0.003
18:3 <i>n</i> -6	0.12±0.002	0.13±0.002	0.12±0.003	0.11±0.003	0.12±0.003	0.11±0.003
18:3 <i>n</i> -4	0.13±0.002	0.11±0.002	0.12±0.003	0.62±0.02	0.5±0.02	0.42±0.02
18:3 <i>n</i> -3	0.69±0.02	0.5±0.01	0.45±0.02	0.07±0.004	0.07±0.002	0.08±0.004
18:3 <i>n</i> -1	0.1±0.01	0.07±0.003	0.07±0.003	1.47±0.06	1.11±0.05	0.98±0.04
18:4 <i>n</i> -3	1.82±0.04	1.54±0.04	1.39±0.06	0.15±0.007	0.13±0.001	0.13±0.01
18:4 <i>n</i> -1	0.17±0.004	0.18±0.01	0.21±0.01	0.29±0.01	0.29±0.01	0.32±0.01
20:2 <i>n</i> -6	0.25±0.004	0.23±0.003	0.21±0.01	0.11±0.01	0.11±0.004	0.1±0.004
20:3 <i>n</i> -6	0.07±0.001	0.07±0.001	0.07±0.002	0.37±0.01	0.34±0.01	0.37±0.01
20:4 <i>n</i> -6	0.33±0.01	0.33±0.01	0.29±0.01	0.12±0.01	0.1±0.003	0.1±0.003
20:3 <i>n</i> -3	0.09±0.003	0.06±0.002	0.07±0.01	0.78±0.03	0.69±0.021	0.61±0.02
20:4 <i>n</i> -3	0.68±0.02	0.5±0.01	0.48±0.02	6.2±0.17	4.69±0.18	4.73±0.14
20:5 <i>n</i> -3	6.98±0.11	7.28±0.15	6.73±0.16	0.42±0.01	0.39±0.01	0.36±0.01
21:5 <i>n</i> -3	0.47±0.004	0.46±0.005	0.42±0.01	0.05±0.002	0.04±0.001	0.044±0.001
22:4 <i>n</i> -6	0.07±0.002	0.08±0.003	0.06±0.004	0.04±0.002	0.05±0.003	0.07±0.004
22:5 <i>n</i> -6	0.12±0.003	0.1±0.002	0.08±0.003	0.11±0.004	0.1±0.01	0.1±0.01
22:4 <i>n</i> -3	0.12±0.002	0.1±0.002	0.09±0.003	0.1±0.002	0.11±0.002	0.1±0.003
22:5 <i>n</i> -3	5.17±0.06	5.23±0.07	4.55±0.11	2.5±0.06	2.57±0.06	2.63±0.07
22:6 <i>n</i> -3	12.05±0.16	10.16±0.18	8.66±0.25	10.29±0.24	8.82±0.21	8.41±0.22
<b>Percentage of total FAs</b>						
Saturated	16.07±0.19	15.1±0.22	14.8±0.29	17.91±0.42	15.45±0.37	15.15±0.37
Monounsaturated	51.31±0.92	54.5±1.13	57.95±1.68	55.5±1.97	61.61±1.78	62.49±1.5
Polyunsaturated	32.63±0.51	30.4±0.57	27.25±0.77	26.59±0.76	22.94±0.67	22.36±0.63

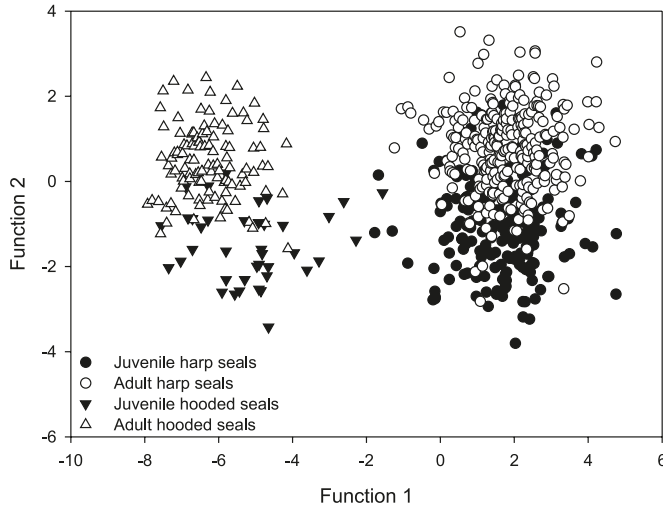
**Note:** Dietary FAs, in normal type, are unmodified FAs that are directly deposited in adipose tissue, whereas primarily dietary FAs, in boldface type, are FAs that are modified at some point between absorption and deposition but whose levels in a predator are highly influenced by consumption of specific prey.

classified to year (Fig. 5). The first discriminant function (70.5% variation in FAs) separated 1994 from 1995 and other years, which formed a cluster, and the second function (9.2% variation in FAs) separated 1994 and 1995.

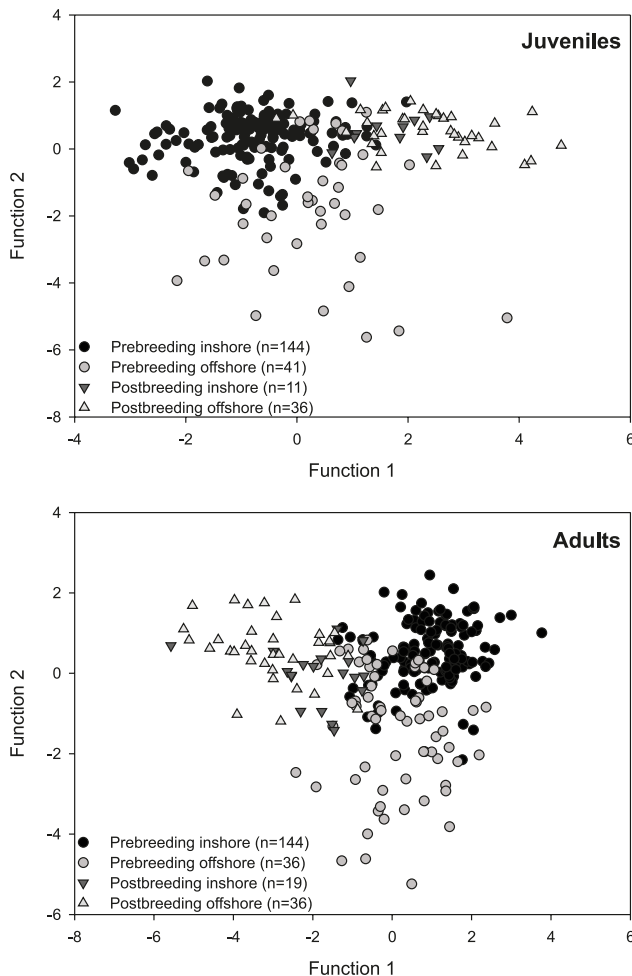
#### **Hooded seals**

We tested for sex, age class, and season as main effects in hooded seals retaining the greatest number of FAs (*n* = 37; 92.5% of total FAs). There was a significant effect of age

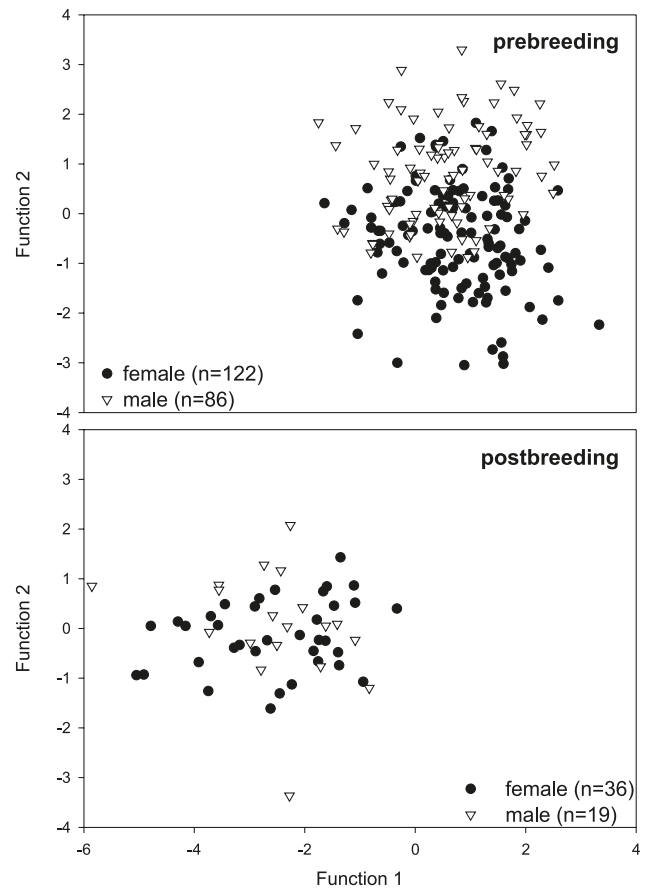
**Fig. 2.** First two discriminant functions for juvenile and adult harp seals (*Pagophilus groenlandicus*; adults,  $n = 294$ ; juveniles,  $n = 232$ ) and hooded seals (*Cystophora cristata*; adults,  $n = 118$ ; juveniles,  $n = 35$ ). Thirty-seven FAs were used in the DFA.



**Fig. 3.** First two discriminant functions for juvenile and adult harp seals (*Pagophilus groenlandicus*) sampled in different seasons and areas. Thirty-one FAs were used in each DFA.



**Fig. 4.** First two discriminant functions for adult male and female harp seals (*Pagophilus groenlandicus*) in pre- and post-breeding seasons. For clarity, pre- and post-breeding animals are shown in separate panels, although scores are from the same DFA. Thirty-one FAs were used.

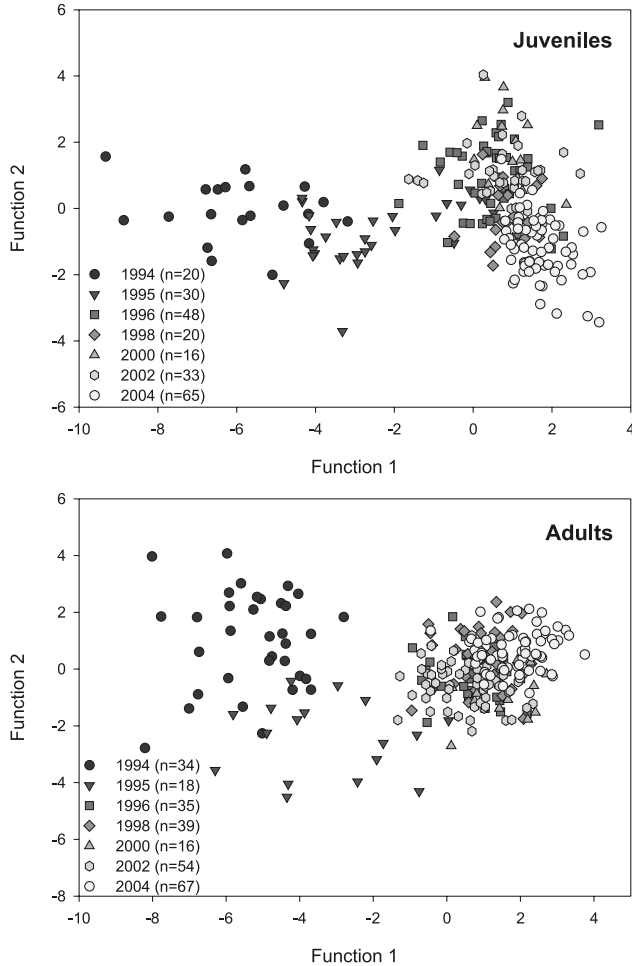


class (Wilks'  $\lambda F_{[36,114]} = 10.28, P < 0.001, \eta^2_{\text{partial}} = 0.77$ ), sex (Wilks'  $\lambda F_{[36,114]} = 2.76, P < 0.001, \eta^2_{\text{partial}} = 0.47$ ), and season (Wilks'  $\lambda F_{[36,114]} = 5.38, P < 0.001, \eta^2_{\text{partial}} = 0.63$ ). Juveniles and adults differed significantly in percentages of 17 of the 37 FAs (MANOVA, test of between-subject effects:  $P < 0.05$  in all cases). Differences were most pronounced in the levels of 20:1 $n$ -7, 22:1 $n$ -9, and 22:1 $n$ -7, which were lower in juveniles. Separate analyses on adults and juveniles revealed that there was no sex effect in juveniles (Wilks'  $\lambda F_{[1,35]} = 90.02, P = 0.083$ ), but there was a significant sex effect in adults (Wilks'  $\lambda F_{[36,77]} = 4.29, P < 0.001, \eta^2_{\text{partial}} = 0.67$ ). Males and females differed significantly in 13 of the 37 FAs (MANOVA, test of between-subject effects:  $P < 0.05$  in all cases). Differences were most pronounced in the levels of 18:3 $n$ -3 and 17:0, which were higher in females.

Using 17 FAs (accounting for 88.9% of FAs), the effect of sampling location on FA profiles of hooded seals was tested by MANOVA with sex, season, and age class as the other main effects. There was a significant effect of sampling location (Wilks'  $\lambda F_{[32,264]} = 5.48, P < 0.001, \eta^2_{\text{partial}} = 0.40$ ), and as above, sex, age class, and season differences were still evident.

DFA on all samples of hooded seals indicate that juveniles differed from adults along the first discriminant function (76.3% variation in FA), while the second discrim-

**Fig. 5.** Discriminant plot of adult and juvenile harp seals (*Pagophilus groenlandicus*) sampled in different years from the prebreeding period. Thirty-one FAs were used in each DFA.



inant function (23.7% variation in FA) separated adult males and adult females. Overall, 87.6% of the grouped cases were classified correctly. Most misclassifications were between adult males and females.

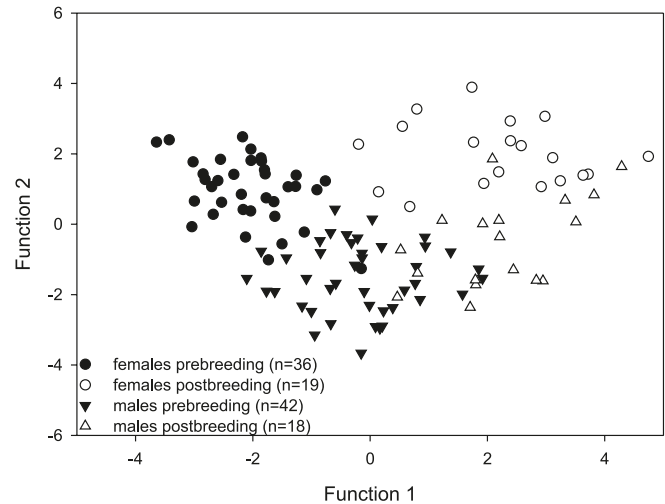
Sex differences in adults persisted in each season with 84.3% of original cases correctly classified (Fig. 6). Pre- and postbreeding animals were separated along the first discriminant function (57.9% variation in FAs), while the sexes were separated along the second discriminant function (36.8% variation in FA). Misclassifications were mostly between sexes rather than seasons (approximately 20% and 10%, respectively).

Sampling location of adult hooded seals was correctly classified in 70.4% of cases. The first function (92% variation in FAs) separated the Greenland samples from the other two areas, while the second function (8% variation in FAs) separated inshore from offshore samples (Fig. 7). However, as Greenland animals were sampled in the summer, this conclusion may be confounded by a seasonal effect. Misclassification of individuals occurred primarily between inshore and offshore samples.

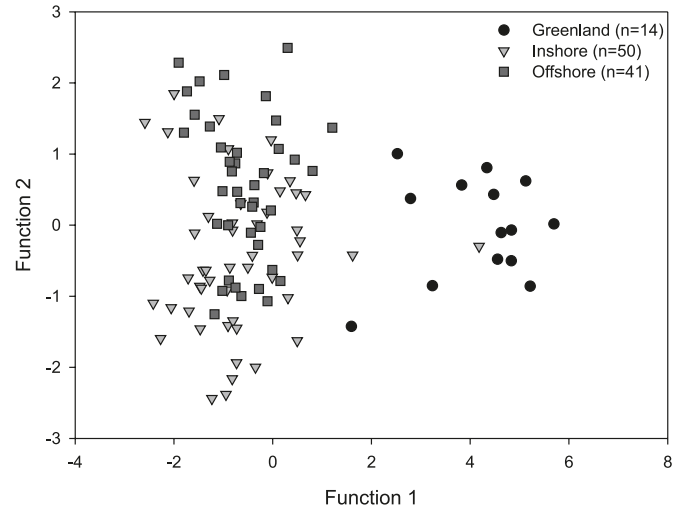
## Discussion

Previous studies have demonstrated that the FA composi-

**Fig. 6.** First two discriminant functions for adult male and female hooded seals (*Cystophora cristata*) in the pre- and post-breeding periods.



**Fig. 7.** First two discriminant functions for adult hooded seals (*Cystophora cristata*) sampled in different areas. Seventeen FAs were used in DFA.



tion of marine mammal blubber is largely determined by diet (e.g., Ackman and Eaton 1966; Iverson 1993; Käkälä et al. 1993; Iverson et al. 1995, 2004; Käkälä and Hyvärinen 1998; Kirsch et al. 2000). When incorporated into a mathematical model, predator and prey FA profiles can be used to produce an estimate of the proportional composition of predator diet (Iverson et al. 2004, 2007). However, trends in predator FA profiles can be used to infer spatial, temporal, and demographic differences in diet (e.g., Iverson et al. 1997; Beck et al. 2005; Budge et al. 2006). For example, statistical differences in FA profiles among demographic groups (Beck et al. 2005) were subsequently shown to represent significant differences in the proportional composition of the diet (Beck et al. 2007). Moreover, as FA data represent longer term feeding (from weeks to months), they may be representative of diet over ecologically significant periods than methods based on the recovery of prey hard structures. Harp and hooded seals undergo two periods of fasting



**Table 4.** Summary of significant main effects (species (harp seal, *Pagophilus groenlandicus*, or hooded seal, *Cystophora cristata*), sex (male or female), age class (juvenile or adult), season (prebreeding or postbreeding), sampling area (inshore or offshore)), number of fatty acids (FA) in the analysis, and partitioning of variance denoted by partial  $\eta^2$  ( $\eta^2_{\text{partial}}$ ) for MANOVAs (all seals, harp seals, hooded seals).

MANOVA	No. of FAs	Significant effects	$\eta^2_{\text{partial}}$
All seals	39	Species	0.77
		Age class	0.37
		Sex	0.15
		Sampling area	0.22
		Season	0.29
Harp seals	31	Age class	0.25
		Sex	0.15
		Sampling area	0.10
		Season	0.35
		Year	0.30
Hooded seals	37	Age class	0.77
		Sex	0.47
		Season	0.63
Hooded seals	17	Age class	0.63
		Sex	0.29
		Sampling area	0.40
		Season	0.35

**Note:** Significant interactions are not shown. Higher values (between 0 and 1) of  $\eta^2_{\text{partial}}$  indicate greater amount of variation accounted for by the model effect.

and subsequent replenishment over an annual cycle (Hammill et al. 1995; Chabot et al. 2006); seals deplete their blubber reserves during reproduction and again during the moult. Thus, the FA composition of seal blubber sampled prior to fasting periods is thought to mainly reflect feeding over the course of several months, with little contribution from feeding earlier in the year. In this study, animals were sampled during nonfasting periods of foraging in open waters or at the beginning of fasting periods (in the case of live-captured biopsied animals). The results of our study show that harp and hooded seals exhibit significant demographic, spatial, and temporal differences in blubber FA profiles and hence diet (Table 4). Although it is tempting to try to infer what kinds of prey are eaten, differences in single dietary FAs cannot be used to reliably identify prey species (Iverson et al. 2004).

We found a significant species effect on FA profiles, indicating marked dietary segregation between harp and hooded seals. These two marine predators are known to dive and forage differently (Folkow and Blix 1999; Folkow et al. 2004). Even in areas where they overlap geographically, hooded seals routinely exceed mean dive depths used by harp seals (Folkow et al. 1996, 2004; G.B. Stenson, unpublished data). Also, in the northwest Atlantic, harp seals spend most of their time over the continental shelf, while hooded seals inhabit the shelf edge (Stenson and Sjare 1997; G.B. Stenson, unpublished data). Data from stomach-content analysis suggest that harp seals consume a mixed diet of pelagic forage fish and invertebrates such as capelin, Arctic cod, herring, euphausiids, and amphipods (Lawson et al. 1995; Lawson and Stenson 1995, 1997). Limited data on diets of hooded seals, although relatively scarce, suggest that

they feed on a mixture of deeper water pelagic and demersal species such as halibut, redfish, and the squid *G. fabricii* with smaller quantities of herring, capelin, Atlantic cod, and Arctic cod (Ross 1993; Kapel 1995; Hammill and Stenson 2000; Potelov et al. 2000; Haug et al. 2007). Even where these species co-occur, (e.g., Greenland Sea), diets differed significantly between species (Haug et al. 2004). Within weeks of being weaned, even young-of-the-year hooded seals routinely dive to depths of 250 m (G.B. Stenson, unpublished data). Thus, interspecific differences in foraging and diving behaviour are manifested at an early age and appear to be maintained as adults. Although differences in FA profiles can arise from variation in the proportion of specific prey consumed, species differences in diving behaviour suggest that dietary segregation in this case is more likely to reflect depth segregation and the consumption of different prey. Such segregation may act to reduce interspecific competition. Spatial segregation and inferred dietary segregation have been found for other pinnipeds (Le Boeuf et al. 1993, 2000; Field et al. 2005; Breed et al. 2006) and seabirds (Weimerskirch et al. 1997; González-Solís et al. 2000).

FA profiles of juveniles differed from those of adults in both harp and hooded seals, but differences were much greater in the hooded seal than in the harp seal. Age-class effects may involve endogenous factors that influence foraging such as body size and energy requirements, physiological and behavioural differences in foraging ability, or may simply reflect differences in spatial distribution. Studies have shown that the physiological and behavioral capacities of juveniles to dive and forage develops over the first year of life (Merrick and Loughlin 1997; Burns et al. 1999; Baker and Donohue 2000; Noren et al. 2005). Thus, we expect that juvenile seals would be limited in their foraging ability relative to adults and presumably have access to fewer or different types of prey, including smaller size classes of particular species, resulting in significant age-class differences in FA profiles. In addition, spatial differences in foraging range have been noted between juveniles and adults of different pinniped species (e.g., Field et al. 2005) including harp seals (Sergeant 1991), which may result in differences in available prey. Indeed, ontogenetic diet shifts have been demonstrated in harp seals, through the analysis of stomach contents, involving an increase in the proportion of forage fish at the expense of pelagic invertebrates (Lawson and Stenson 1995). Little is known about ontogenetic diet shifts in hooded seals based on the sampling of stomach contents. However, our results indicate that ontogenetic variation in diet is an important component of dietary niche breadth of hooded seals.

Sex differences in foraging behaviour and diet are assumed to reflect differences in sex-specific costs of reproduction, or in the case of size dimorphism, effects of larger body size and intraspecific competition. However, it is difficult to tease these two factors apart. Telemetry studies have not revealed any obvious differences in movement or diving behaviour between male and female harp seals (G.B. Stenson, unpublished data). However, male and female hooded seals have been noted to display differences in mean dive depths in the postbreeding period (C.E. Bajzak, D. Côté, M.O. Hammill, and G.B. Stenson, unpublished data). Sex differences in diet have been found in both monomorphic (e.g., Lewis et al. 2002) and dimorphic (e.g., Clarke et al.

1998) animal species including pinnipeds (e.g., Beck et al. 2007). Although we found significant differences in FA profiles between adult males and females in both species, sex accounted for little of the variation in FA profiles of harp seals where males are only slightly larger than females. Larger sex differences in body size in hooded seals were associated with larger differences in FA profiles between males and females. No sex differences were found for juvenile animals. There was a difference in FA profiles between the pre- and post-breeding periods for both species; however, sex differences were not as pronounced in the post-breeding period in harp seals as they were during the prebreeding period. The magnitude of sex differences found in harp seals was relatively small compared with the size-dimorphic hooded seals and grey seals (Beck et al. 2005). As juveniles lack sex differences in diets, do not have reproductive costs, and exhibit little body-size dimorphism, we hypothesize that sex differences in the diets of adult harp seals in the prebreeding period are related to sex-specific costs associated with reproduction. Although this may also be true for hooded seals, divergent diets of males and females may also reflect the increased costs of maintaining a larger body size in males, which may help to explain the greater degree of divergence within both pre- and post-breeding animals, respectively.

As referred to above, we noted significant variation in FA profiles in both harp and hooded seals between pre- and post-breeding sampling periods. Seasonal differences have been identified in diets of harp seals based on stomach-content analysis primarily in the proportions of Arctic cod, capelin, northern sand lance (*Ammodytes dubius* Reinhardt, 1837), and invertebrates (Hammill and Stenson 2000). Seasonal differences in diets have been observed in other pinniped species and have been linked to seasonal changes in prey availability (e.g., Brown and Pierce 1998; Hall et al. 1998; Wathne et al. 2000). Without specific information on distribution and abundance of prey, it is unclear whether overall seasonal differences in FA profiles were related to prey availability, or to specific prey selection owing perhaps to varying energetic demands.

We also noted a significant effect of sampling location in FA profiles for both species. However, in harp seals, the effect was less pronounced in the postbreeding (April–May) period perhaps owing to a more restricted foraging range prior to the molt, or reduced prey availability. Although there were some misclassifications, the spatial effect suggests that diets differ geographically for both adults and juveniles. Data from stomach-content analysis has previously indicated distinct differences between inshore and offshore diets for harp seals (Lawson et al. 1995, 1998; Lawson and Stenson 1997): inshore diets tended to be dominated by capelin, herring, and Arctic cod, while offshore diets tended to be dominated by invertebrates, capelin, sand lance, and a mix of demersal species. Recent ship-based observations and satellite tagging has revealed that seals are found in offshore areas in higher numbers than previously thought and that these areas appear to be important to wintering harp seals (Stenson and Sjare 1997; Lacoste and Stenson 2000). The effect of sampling location on FA profiles implies that seals were resident long enough in these areas to reflect differences in diet.

Less is known about regional variation in diets of hooded

seals through traditional sampling, although near and offshore differences have been observed (Hammill and Stenson 2000). Most notably, inshore diets had higher proportions of Arctic cod, herring, and redfish, while offshore diets had higher proportions of Atlantic cod, flounders (Pleuronectidae), grenadiers (Macrouridae), blue hake (*Antimora rostrata* (Günther, 1878)), and the squid *G. fabricii*. In hooded seals, most misclassifications were between inshore and offshore samples from Newfoundland and Labrador waters. Although hooded seals are considered offshore, deepwater foragers, we did obtain samples in the inshore in the late-winter months. We expect that these animals were either foraging in deepwater trenches that come close to shore along the northeast coast of Newfoundland (Fig. 1) or moving south, following the formation of pack ice in anticipation of the breeding season on the “Front” in March. As peak energy reserves are typically obtained by February for both males and females (Chabot et al. 2006), it is equally likely that these inshore sampling locations are not important foraging areas for the population of hooded seals as a whole; thus, we hypothesize that FA profiles represented assimilated diets from more distant areas. That being said, the samples obtained from eastern Greenland in summer were clearly distinct from Newfoundland and Labrador samples along the first discriminant function (92% of variance in FA profiles), suggesting that there is large-scale variation in diets of hooded seals over the annual migration cycle. Stomach contents collected in the Greenland Sea indicate that hooded seals feed primarily on the squid *G. fabricii*, as well as Arctic cod to a lesser degree (Potelov et al. 2000; Haug et al. 2007). A more fish-based diet including Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum, 1792)), Atlantic cod, and redfish has been found in Newfoundland and Labrador waters (Hammill and Stenson 2000).

We found pronounced interannual differences in FA profiles of harp seals between the mid-1990s and the late 1990s – 2000s. Small sample sizes in most years precluded interannual analysis in hooded seals. During the last decade, large ecological changes have occurred in the northwest Atlantic. The once abundant Atlantic cod stocks off Newfoundland were decimated by the early 1990s owing to overfishing (Rose 2004). As well, abundance and distribution of many important forage species, including Arctic cod and capelin, have changed significantly (particularly inshore) since the mid-1990s (Lilly and Simpson 2000; Carscadden et al. 2001; Rose 2004; Frank et al. 2005). Essentially, capelin, a former principle prey of seals, cod, whales, and seabirds, has declined in northern areas since the 1990s (Carscadden et al. 2001; Rose 2004). Capelin became scarce along the coast of Labrador and the Grand Banks, while abundance increased on the Flemish Cap and the Scotian Shelf (Lilly and Simpson 2000; Carscadden et al. 2001). Concurrently, Arctic cod distribution shifted southward from Labrador to coastal Newfoundland and the Grand Banks out to the shelf edge. This expansion in distribution and biomass of Arctic cod peaked in 1995 (Lilly and Simpson 2000). In 1998–1999, Arctic cod appeared to be returning to northerly distributions observed previously (Lilly and Simpson 2000). However, by 2000, capelin had not returned to waters off the Labrador coast (Department of Fisheries and Oceans 2001). While acoustic research surveys of pelagic forage fish were re-

sumed in 1999, these have been very limited in area; essentially there has been no assessment in offshore waters since the early 1990s. Moreover, direct assessments of stocks through trawl surveys have not been performed since 2000 (Department of Fisheries and Oceans 2000), resulting in a significant gap in our understanding of the current dynamics of this perturbed ecosystem.

Although it is not possible to attribute the influence of a particular prey species to changes in FA profiles, the trends in our data are coincident with these large changes in prey availability that occurred in the mid-1990s. It would appear that diets of harp seals have been fairly constant since that time, as signatures have changed little between 1996 and 2004 relative to the previous 2 years. Patterns were similar in juvenile and adult animals. We found a significant interaction between sex and year, suggesting that the sexes responded in a different manner to this large-scale environmental variability. However, without knowing the diet of each sex, it is difficult to interpret this interaction.

The divergence among demographic groups noted here lends support to the idea of both inter- and intra-specific dietary segregation for harp and hooded seals. However, intra-specific effects appear larger in hooded seals, which over their life history, display a greater range in body size than do harp seals owing to sexual size dimorphism in adults. Unlike studies on terrestrial predator guilds, few studies have comparatively documented ontogenetic diet differences for sympatric marine predators. This is due to the difficulty of making observations or obtaining stomach samples over large foraging ranges. An integrative biochemical approach such as FA profiles reduces this bias, since they represent the assimilated portion of the diet over periods of months — an ecologically relevant time scale — not simply the last meal (Iverson et al. 2004). Thus our data is not merely an affirmation of what is already known but represent a significant contribution, albeit a first step, to our understanding of diet selection for these predators. The independent inferences from FA profiles considerably strengthens evidence for the influence of various intrinsic and extrinsic effects on the diets of harp and hooded seals.

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