# Unusual fatty acid biomarkers reveal age- and sex-specific foraging in polar bears (*Ursus maritimus*)

**G.W. Thiemann, S.M. Budge, S.J. Iverson, and I. Stirling**

**Abstract:** We used fatty acid (FA) biomarkers in a novel approach to study the foraging habits of a top predator. We tested the hypothesis that non-methylene-interrupted FA (NMI FA), synthesized by benthic molluscs, are transferred via pinnipeds to polar bears (*Ursus maritimus* Phipps, 1774) at the top of the arctic marine food web. Among eight species of marine mammals preyed upon by polar bears, NMI FA were prevalent only in benthic-feeding bearded seals (*Erignathus barbatus* (Erxleben, 1777)) and Atlantic walruses (*Odobenus rosmarus rosmarus* (L., 1758)). These two prey species differed in their relative proportions of NMI FA — $22:2\Delta7,15$ was almost exclusive to bearded seals, whereas $20:2\Delta5,11$ was most abundant in Atlantic walruses. Six different NMI FA were identified in polar bears. Trends in individual NMI FA showed that large, adult male polar bears were the primary predators of bearded seals and Atlantic walruses. These findings were confirmed through quantitative FA signature analysis (QFASA) using an entirely different set of FA. In addition to corroborating the accuracy of QFASA diet estimates, these results indicate that individual NMI FA can provide specific information on polar bear foraging and therefore provide insights into the bottom–up effects of environmental change in arctic ecosystems.

**Résumé :** Nous utilisons des acides gras (FA) comme biomarqueurs dans une méthodologie nouvelle pour l'étude des habitudes alimentaires d'un prédateur de niveau supérieur. Nous testons l'hypothèse selon laquelle les FA sans interruption méthylénique (NMI FA) synthétisés par les mollusques benthiques sont transférés via les pinnipèdes aux ours polaires (*Ursus maritimus* Phipps, 1774) au sommet du réseau alimentaire marin de l'Arctique. Chez les huit espèces de mammifères marins servant de proies aux ours polaires, les NMI FA ne sont présents en quantité que chez le phoque barbu (*Erignathus barbatus* (Erxleben, 1777)) et le morse de l'Atlantique (*Odobenus rosmarus rosmarus* (L., 1758)) qui se nourrissent de benthos. Ces deux espèces de proies diffèrent par leurs proportions relatives de NMI FA — le $22:2\Delta7,15$ se retrouve presque exclusivement chez le phoque barbu, alors que le $20:2\Delta5,11$ est le plus abondant chez le morse de l'Atlantique. Six NMI FA différents se reconnaissent chez l'ours polaire. Les tendances observées chez les différents NMI FA montrent que les ours polaires adultes mâles de grande taille sont les prédateurs principaux des phoques barbus et des morses de l'Atlantique. Ces résultats sont corroborés par une analyse quantitative des signatures des FA (QFASA) qui utilise un ensemble différent de FA. En plus de confirmer la justesse des estimations du régime alimentaire faites par QFASA, nos résultats indiquent que des NMI FA individuels peuvent fournir des renseignements spécifiques sur l'alimentation des ours polaires et, par conséquent, ouvrir des perspectives sur les effets ascendants des changements environnementaux dans les écosystèmes arctiques.

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## Introduction

Top predators, because of their long lifespan and wide geographic distribution, may provide an indication of ecosystem functioning over large temporal and spatial scales. Understanding the relationships between predators and prey may be especially important for arctic ecosystems because recent environmental change appears to be altering food webs (Gaston et al. 2003). Although dietary studies based on prey remains (e.g., Derocher et al. 2002), stable isotope ratios (e.g., Holst et al. 2001), or fecal- and stomach-content analyses (e.g., Lowry et al. 1980) have provided valuable data on the diets of arctic predators, these techniques have well-documented biases and limitations (Gearing 1991; Bowen 2000; Derocher et al. 2002). Consequently, fatty acid (FA) signature analysis is becoming widely used, both alone and in conjunction with other methods, to examine the qualitative and quantitative characteristics of predator diets (e.g., Pond et al. 1995; Iverson et al. 1997, 2004).

Marine ecosystems contain a wide array of FA and biochemical limitations on their synthesis in mammalian predators result in many dietary FA being directly or predictably incorporated into consumer adipose tissue (Ackman and Eaton 1966; Iverson et al. 1995; Dalsgaard and St. John 2004). As a result, the relative abundance of multiple FA in the

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adipose stores of a predator (i.e., its FA signature) can provide information on diet integrated over weeks to months (Kirsch et al. 2000; Iverson et al. 2004). Quantitative FA signature analysis (QFASA) of predators and their prey provides a powerful ecological tool for estimating the diets of free-ranging animals (Iverson et al. 2004, 2006). Although this approach generates a quantitative estimate of diet for each predator, it requires extensive sampling of all or most potential prey species, as well as a complex statistical model. Qualitative comparisons of predator FA signatures, in the absence of statistical modeling, can indicate spatial and temporal differences in overall foraging, as well as the ecological (e.g., productivity, climate) and demographic (e.g., age, sex) factors affecting such differences (e.g., Pond et al. 1995; Raclot et al. 1998; Beck et al. 2005). However, because most FA are common to all prey species, these types of qualitative comparisons often provide little insight into the specific prey species being consumed.

Although the presence of specific FA biomarkers is in principle rare, Budge et al. (2007) recently identified a group of unusual, non-methylene-interrupted FA (NMI FA) in the blubber of bearded seals (*Erignathus barbatus* (Erxleben, 1777)) and Pacific walruses (*Odobenus rosmarus divergens* (Illiger, 1815)) in the Bering Strait. These NMI FA, with carbon chain lengths of 20 or 22, are characterized by the presence of more than one methylene group between ethylenic bonds and are produced endogenously by benthic molluscs (Joseph 1982), including mussels (*Mytilus edulis* L., 1758; Paradis and Ackman 1977), oysters (*Crassostrea virginica* (Gmelin, 1791) and *Ostrea edulis* L., 1758; Watanabe and Ackman 1972), and clams (*Mercenaria mercenaria* (L., 1758); Klingensmith 1982), among others (Ackman and Hooper 1973; Ackman et al. 1974; Takagi et al. 1980; Zhukova 1986).

Considering the unusual structure of NMI FA and their origins at the base of the food web, Paradis and Ackman (1977) suggested that these compounds may serve as trophic biomarkers — compounds transferred through the food web without biochemical modification. NMI FA have been identified in the adipose stores of predators that are known to forage on molluscs, including starfish (*Asterias vulgaris* Verrill, 1866 (= *Asterias rubens* L., 1758); Paradis and Ackman 1977), Kemp's Ridley sea turtles (*Lepidochelys kempii* (Garman, 1880); Ackman et al. 1971), and Atlantic sturgeon (*Acipenser oxyrinchus* Mitchill, 1815; Ackman et al. 1975). The distinctly different NMI FA profiles observed in benthic-feeding bearded seals and Pacific walruses indicate that the two species exploit largely different prey resources in the Bering Sea (Budge et al. 2007).

We are aware of no reported observations of polar bears (*Ursus maritimus* Phipps, 1774) feeding directly on the benthic molluscs that synthesize NMI FA. Furthermore, although polar bears commonly prey on marine mammals that feed on benthic invertebrates, including bearded seals (Stirling and Archibald 1977; Smith 1980) and walruses (Calvert and Stirling 1990), they rarely eat the contents of the body cavity, so potential second-hand ingestion of benthic invertebrates from that source would be extremely rare. Here, we test the hypothesis that NMI FA are transferred from benthic molluscs via marine mammals to polar bears at the top of the arctic marine food web. We examine

the abundance of NMI FA in the blubber stores of marine mammals preyed upon by polar bears across the Canadian Arctic. By comparing NMI FA concentrations with polar bear diets as estimated by QFASA, we use individual FA biomarkers in a novel way to examine age- and sex-specific foraging in a top predator.

## Materials and methods

### Sample collection

Adipose tissue samples were collected from arctic marine mammals ($n = 311$) and polar bears ($n = 779$) across the Canadian Arctic (Fig. 1). Pinnipeds and cetaceans were sampled from 1992 to 2004 in the Southern Beaufort Sea, Northern Beaufort Sea, Lancaster Sound, Foxe Basin, Western Hudson Bay, and Davis Strait (Table 1). Polar bears were sampled from 2001 to 2004 in Southern Beaufort Sea, Northern Beaufort Sea, Foxe Basin, Western Hudson Bay, Southern Hudson Bay, Baffin Bay, and Davis Strait (Table 2). Although pinnipeds and cetaceans were sampled opportunistically over several years, interannual differences in FA signatures within species are generally small relative to differences between species (Iverson et al. 2002; Thiemann et al. 2007). For some regional comparisons, samples from the northern and southern Beaufort Sea were pooled into a single Beaufort Sea region.

Full-depth blubber samples were collected from eight potential polar bear prey species: bearded seals ($n = 78$), ringed seals (*Phoca hispida* Schreber, 1775 (= *Pusa hispida* (Schreber, 1775)); $n = 63$), harbour seals (*Phoca vitulina* L., 1758; $n = 18$), harp seals (*Pagophilus groenlandicus* (Erxleben, 1777)); $n = 20$), hooded seals (*Cystophora cristata* (Erxleben, 1777); $n = 6$), Atlantic walruses (*Odobenus rosmarus rosmarus* (L., 1758); $n = 43$), narwhals (*Monodon monoceros* L., 1758; $n = 17$), and beluga whales (*Delphinapterus leucas* (Pallas, 1776); $n = 66$). Animals were shot nonselectively by Inuit hunters or sampled by other researchers studying arctic marine mammals. Samples were wrapped in foil and transported frozen to the laboratory where a full-depth subsample was taken through the center of each sample, an area that is protected from oxidation during frozen storage (Budge et al. 2006).

Free-ranging polar bears ($n = 559$) were sampled during the course of long-term population studies in the Beaufort Sea and Hudson Bay. Bears were located from a Bell 206B JetRanger helicopter and immobilized with Telazol® (Fort Dodge Laboratories, Fort Dodge, Iowa) following standard chemical immobilization protocols (Stirling et al. 1989). Adipose tissue samples were collected using a 6 mm biopsy punch and consisted of a full-layer core from skin to muscle, taken approximately 15 cm lateral to the base of the tail. Tissue samples were stored frozen in airtight containers until analysis (<6 months), and all immobilization and live-capture procedures were annually reviewed and approved by the Animal Care Committee of the Canadian Wildlife Service, Prairie and Northern Region, Edmonton, Alberta. An additional 220 adipose tissue samples were collected from bears harvested by Inuit hunters during annual subsistence hunts. Of the samples collected from harvested bears, 52 did not have accompanying age data. Since it is illegal to shoot dependent cubs and weaning occurs approximately

**Fig. 1.** Canadian polar bear (*Ursus maritimus*) populations where samples were collected in this study: Southern Beaufort Sea (SB), Northern Beaufort Sea (NB), Lancaster Sound (LS), Foxe Basin (FB), Western Hudson Bay (WH), Southern Hudson Bay (SH), Baffin Bay (BB), and Davis Strait (DS).
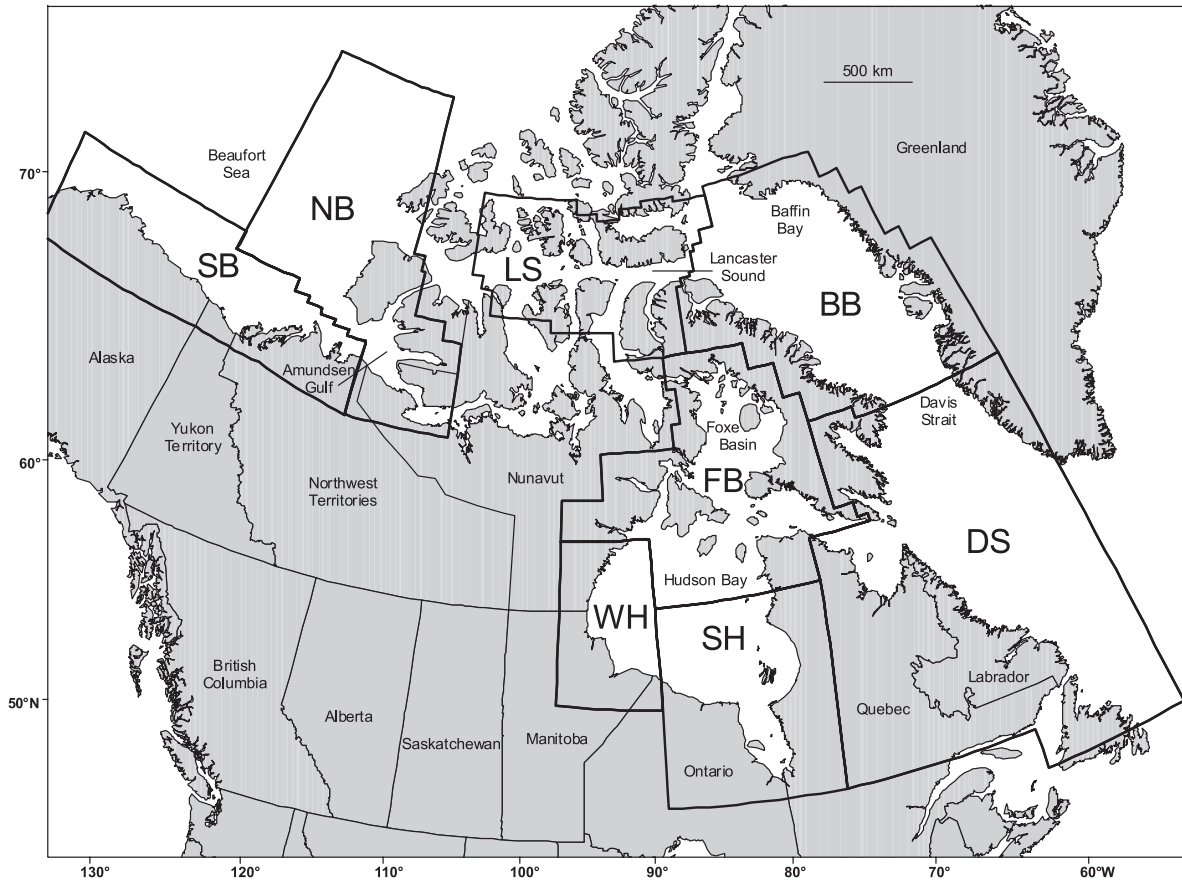


**Table 1.** Distribution of marine mammals sampled from 1992 to 2004.

| Species | Total | Region | | | | |
| --- | --- | --- | --- | --- | --- | --- |
| | | Beaufort–Amundsen* | Lancaster Sound | Foxe Basin | W. Hudson Bay | Davis Strait |
| Bearded seal (*Erignathus barbatus*) | 78 | 20 | 0 | 0 | 12 | 46 |
| Ringed seal (*Phoca hispida = Pusa hispida*) | 63 | 25 | 0 | 0 | 20 | 18 |
| Harbour seal (*Phoca vitulina*) | 18 | 0 | 0 | 0 | 18 | 0 |
| Harp seal (*Pagophilus groenlandicus*) | 20 | 0 | 0 | 0 | 0 | 20 |
| Hooded seal (*Cystophora cristata*) | 6 | 0 | 0 | 0 | 0 | 6 |
| Narwhal (*Monodon monoceros*) | 17 | 0 | 10 | 7 | 0 | 0 |
| Beluga whale (*Delphinapterus leucas*) | 66 | 19 | 8 | 16 | 9 | 14 |
| Atlantic walrus (*Odobenus rosmarus rosmarus*) | 43 | 0 | 0 | 43 | 0 | 0 |
| Total | 311 | 64 | 18 | 66 | 59 | 104 |

**Note:** Locations correspond to Canadian polar bear management zones illustrated in Fig. 1.

*Samples pooled from the northern and southern Beaufort Sea regions.

2.5 years after birth, these samples were assumed to have come from bears at least 2.5 years old and are referred to as "harvested" bears (Table 2). Based on the overall age distribution of hunter-killed bears (61% adult), these samples likely represented mainly adults. Other bears were classified as adults (5 years +), subadults (3–4 years), independent cubs (weaned yearling or 2-year-old), and dependent cubs (cub of the year (COY), yearling, or 2-year-old

with its mother). Sampled polar bears ranged in age from COY to 29 years.

## Lipid analysis

Lipid was quantitatively extracted from each tissue sample (Iverson et al. 2001; Budge et al. 2006) and FA methyl esters (FAME) prepared from 100 mg of pure extracted lipid using $H_2SO_4$ as a catalyst (Thiemann et al. 2004). Duplicate

**Table 2.** Distribution of polar bears sampled from 2001 to 2004.

| Polar bear | Total | Region | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | S. Beaufort | N. Beaufort | Foxe Basin | W. Hudson Bay | S. Hudson Bay | Baffin Bay | Davis Strait |
| Adult female | 216 | 58 | 49 | 9 | 49 | 39 | 8 | 4 |
| Adult male | 265 | 55 | 33 | 21 | 59 | 44 | 40 | 13 |
| Harvested female* | 13 | 0 | 0 | 2 | 5 | 0 | 6 | 0 |
| Harvested male* | 39 | 0 | 0 | 13 | 10 | 1 | 8 | 7 |
| Subadult | 129 | 27 | 12 | 19 | 17 | 32 | 11 | 11 |
| Dependent cub | 32 | 5 | 4 | 2 | 20 | 1 | 0 | 0 |
| Independent cub | 85 | 24 | 43 | 0 | 17 | 1 | 0 | 0 |
| Total | 779 | 169 | 141 | 66 | 177 | 118 | 73 | 35 |

**Note:** Locations correspond to Canadian polar bear management zones illustrated in Fig. 1.

*Independent-age bears (>2.5 years) harvested by Inuit subsistence hunters.

analyses and identification of all FAME were performed using temperature-programmed gas–liquid chromatography according to Iverson et al. (1997, 2004). Samples were analyzed on a Perkin Elmer Autosystem II Capillary gas chromatograph with a flame ionization detector fitted with a flexible fused silica column (30 m × 0.25 mm inner diameter) coated with 50% cyanopropyl polysiloxane (0.25 µm film thickness; Agilent Technologies, DB-23, Palo Alto, California). FA data are expressed as the mass percentage of total FA ± SE. Regular methylene-interrupted FA are referred to by carbon chain length : number of double bonds, and position of the first double bond relative to the terminal methyl group. In NMI FA, the positions of non-methylene bonds cannot be assumed and all bond positions are specified using a delta ($\Delta$) system. Six different NMI FA were identified using a combination of retention times, published chromatograms (Ackman and Hooper 1973; Paradis and Ackman 1977; Ackman 1986; Fang et al. 1993), and silver nitrate (argentation) chromatography (Iverson et al. 2001, 2002; Budge et al. 2007). NMI FA structures were confirmed by gas chromatograph – mass spectrometry. Because NMI FA are prominent in bivalves, we used extracts of *M. edulis* as laboratory standards. Those FA accounting for at least 0.01% of total FA could be reliably identified and quantified in a given sample. The precise location of double bonds in one of the 22-carbon non-methylene-interrupted dienes could not be fully determined; it is therefore referred to as 22:2NMID.

### Statistical analyses

FA data were transformed to improve normality by calculating the log of the ratio of each FA to 18:0 (Budge et al. 2006) and species-specific differences in the relative abundance of the six NMI FA were examined using multivariate analysis of variance (MANOVA). Effects of age class, geographic region, and sex on the abundance of NMI FA in polar bears were tested using fixed-effects MANOVA or ANOVA. To examine the potential relationship between body size and abundance of $22:2\Delta7,15$ in polar bears, we performed linear regression on data from live-captured, adult polar bears in the Beaufort Sea, Western Hudson Bay, and Southern Hudson Bay. Regression analyses were performed on males and females separately to account for sex differences in body mass, which was calculated from the relationship between chest girth and body mass (Kolenosky et al.

1989; Derocher 1991). All statistical analyses were performed using SPSS® for Windows® version 10.1 (SPSS Inc. 2000).

### Quantitative fatty acid signature analysis

To examine potential dietary sources of NMI FA in polar bears, we performed QFASA modeling on the FA signatures of all individual polar bears following the methods of Iverson et al. (2004, 2006). We used 31 FA that are derived exclusively or largely from the diet (Iverson et al. 2004; Thiemann 2006) and calibration coefficients developed through captive feeding studies of mink (*Mustela vison* Schreber, 1777) (see Iverson et al. 2006; Thiemann 2006). No NMI FA were used in the QFASA modeling to maintain independence of comparisons. To estimate diets, the QFASA model applies the calibration coefficients to each predator signature to account for FA-specific differences in predator metabolism. It then determines the most likely combination of prey FA signatures that comes closest to matching the observed calibrated predator (Iverson et al. 2004). Polar bears from the seven populations studied here were modeled on a larger prey database of 843 samples and bears in each region were modeled using the prey species available in that area. Correlation analyses were performed to examine the relationship between NMI FA concentration (log-transformed) and polar bear diets (arcsine-transformed proportional data; Zar 1999) as estimated by QFASA.

## Results

### NMI FA in seals, walruses, and whales

NMI FA were not detected in the blubber of harp seals, hooded seals, beluga whales, or narwhals. Six different NMI FA were identified in the blubber of bearded seals, harbour seals, ringed seals, and Atlantic walruses, and the relative abundance of NMI FA differed between species (MANOVA: Wilks' $\lambda = 0.020$, $P < 0.001$; Fig. 2A). Walruses had the highest levels of five of the six NMI FA (Bonferroni-adjusted $P < 0.008$) and were characterized by particularly high levels of $20:2\Delta5,11$ ($0.42\% \pm 0.02\%$; mean ± SE). Bearded seals had by far the greatest amount of $22:2\Delta7,15$ ($0.46\% \pm 0.03\%$): more than 38 times greater than that in ringed seals, the next highest species. Ringed seals tended to have the lowest level of most NMI FA,

**Fig. 2.** Abundance of non-methylene-interrupted fatty acids (NMI FA; mass percentage of total FA + SE) in (A) bearded seals (*Erignathus barbatus*), harbour seals (*Phoca vitulina*), ringed seals (*Phoca hispida = Pusa hispida*), and Atlantic walruses (*Odobenus rosmarus rosmarus*) sampled across the Canadian Arctic and (B) bearded seals sampled in northern and southern Beaufort Sea (pooled), Western Hudson Bay, and Davis Strait. Levels of NMI FA in samples from harp seals (*Pagophilus groenlandicus*), hooded seals (*Cystophora cristata*), beluga whales (*Delphinapterus leucas*), and narwhals (*Monodon monoceros*) were undetectable.
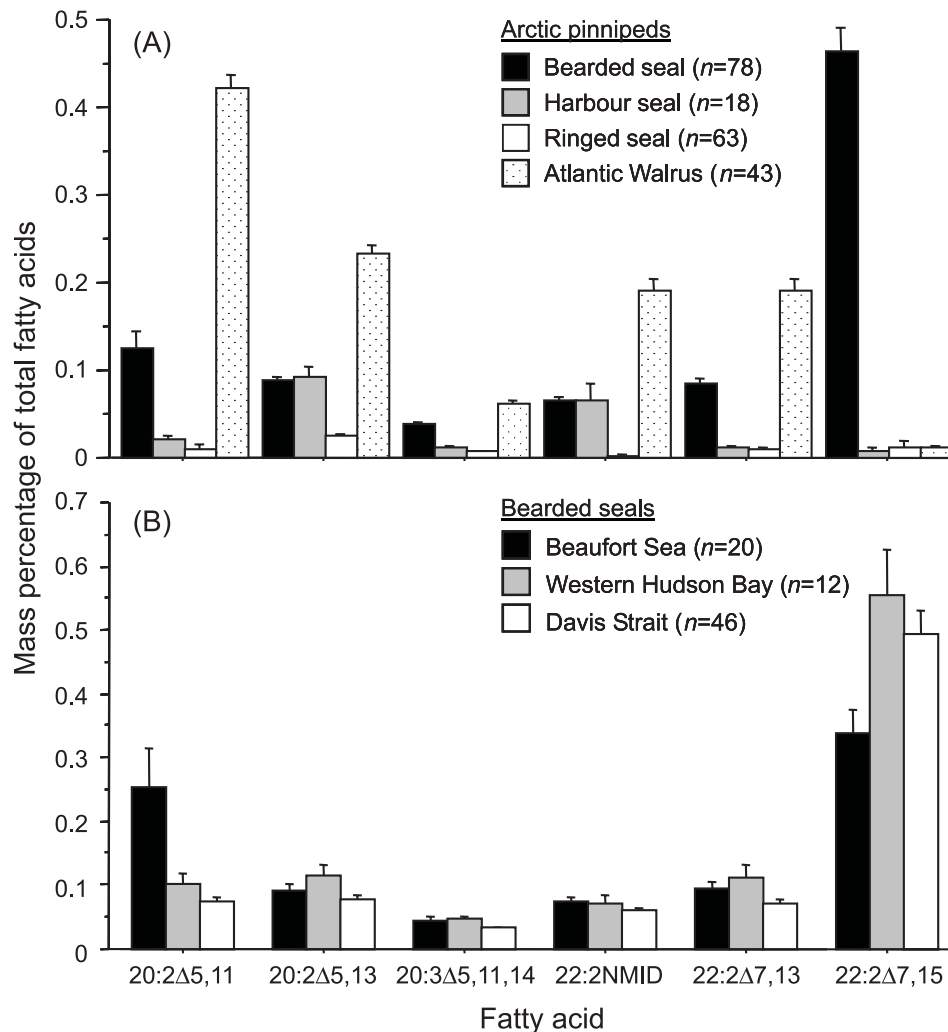


although they did not differ significantly from harbour seals for four of the six FA.

Although bearded seals across the Canadian Arctic were characterized by high levels of 22:2Δ7,15 relative to all other species, their NMI FA profiles differed regionally (MANOVA: Wilks' $\lambda = 0.343$, $P < 0.001$; Fig. 2B). Bearded seals in the Beaufort Sea were most distinctive and had more 20:2Δ5,11 than seals in Western Hudson Bay or Davis Strait ($P < 0.001$). Although bearded seals in the Beaufort Sea tended to have less 22:2Δ7,15 than those in Western Hudson Bay or Davis Strait, the differences were not statistically significant (Bonferroni-adjusted $P > 0.017$).

**NMI FA in polar bears**

NMI FA were clearly present, albeit in low absolute levels, in the adipose tissue of polar bears. Age had a significant effect on the relative abundance of NMI FA (MANOVA: Wilks' $\lambda = 0.732$, $P < 0.001$; Fig. 3A), with adult and harvested bears having higher levels than juvenile bears. There were no differences among juvenile age classes

(subadult, independent cub, and dependent cub) for any of the six NMI FA.

Because NMI FA were present in small amounts in juvenile bears, only adult and harvested bears (which included some adults) were used to examine variability by sex and region (two-way MANOVA). Levels of NMI FA differed significantly by sex (Wilks' $\lambda = 0.854$, $P < 0.001$; Fig. 3A) and all six NMI FA were significantly more abundant in males than in females ($P < 0.010$). Although there were significant regional differences in NMI FA levels (Wilks' $\lambda = 0.255$, $P < 0.001$; Fig. 3B), there were no clear geographic trends across all FA.

Because 20:2Δ5,11 and 22:2Δ7,15 dominated the NMI FA profiles of Atlantic walruses and bearded seals, respectively (Fig. 2A), these FA were examined in greater detail in polar bears. Two-way ANOVA showed that both FA were more abundant in male bears than in female bears ($P < 0.001$) and both exhibited significant regional differences ($P < 0.001$; Fig. 4). The NMI FA 20:2Δ5,11 was most abundant in polar bears in the Beaufort Sea and Foxe Basin

**Fig. 3.** Abundance of NMI FA (mass percentage of total FA + SE) in (A) polar bears of different age classes sampled across the Canadian Arctic and (B) adult and harvested (>2.5 years) polar bears in seven Canadian populations. NMI FA profiles differed significantly by age ($P < 0.001$), sex ($P < 0.001$), and region ($P < 0.001$).
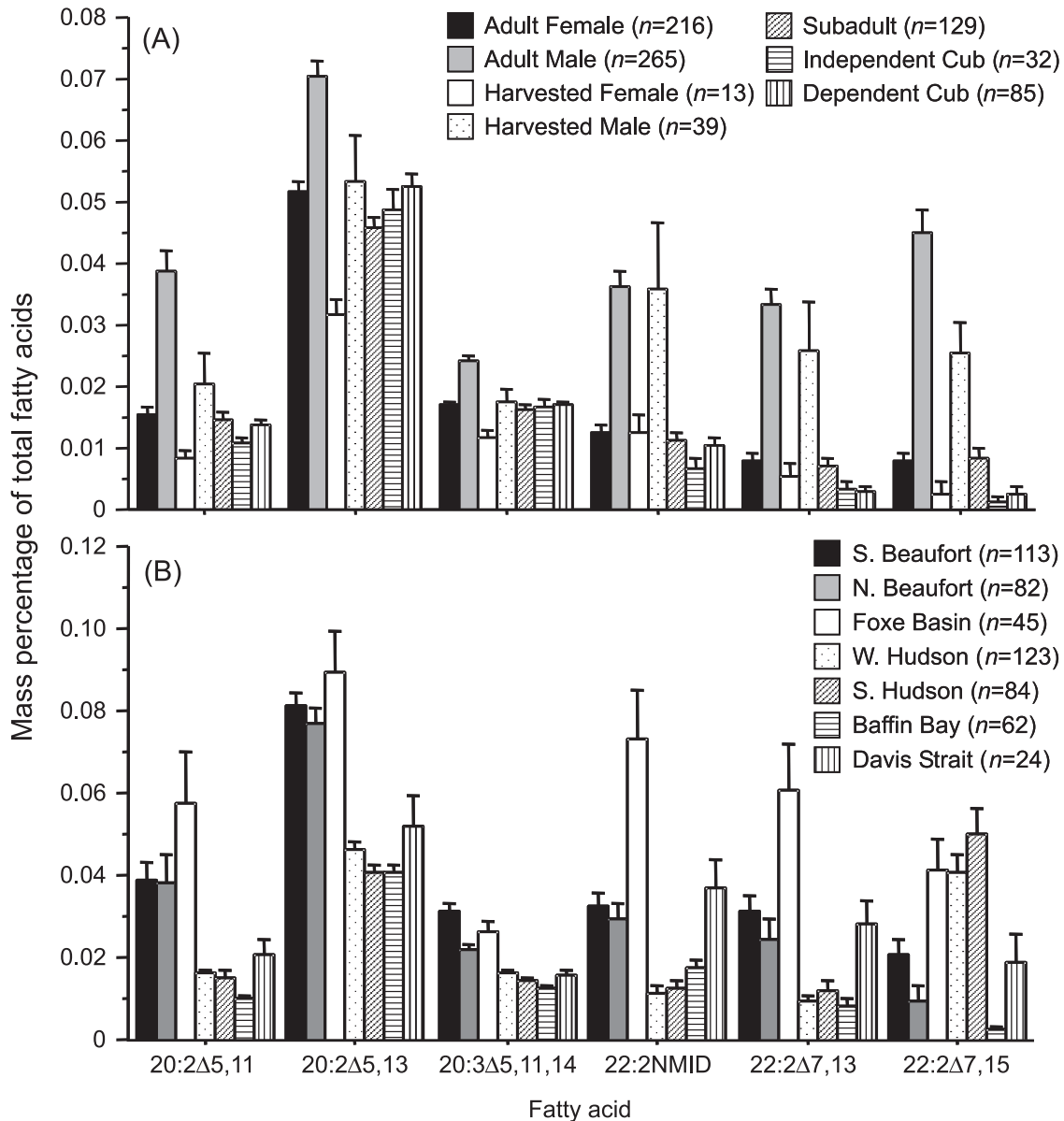


(Fig. 4A), whereas 22:2Δ7,15 was highest among bears in Hudson Bay and Foxe Basin (Fig. 4B). All walrus samples were collected in Foxe Basin and, in this region, 20:2Δ5,11 was most abundant in adult male bears (ANOVA: sex, $P = 0.018$; age, $P = 0.049$). Polar bears in Baffin Bay had particularly low levels of 22:2Δ7,15. Significant sex × region interactions ($P < 0.040$) in the abundance of both FA were driven by generally low levels and little variability in these NMI FA among females.

There was a significant positive relationship between the abundance of 22:2Δ7,15 and adult body mass in male polar bears in the Southern Beaufort Sea ($P < 0.001$; Fig. 5) and among males and females in Western Hudson Bay ($P < 0.012$). There was no sex-specific effect of body mass on 22:2Δ7,15 levels in polar bears in the Northern Beaufort Sea, Southern Hudson Bay, or in females in the Southern

Beaufort Sea. However, when adult males and females were pooled, there was a significant ($P < 0.001$) relationship between body mass and 22:2Δ7,15 concentration in all four populations.

According to QFASA estimates, bearded seal and Atlantic walrus biomass accounted for 14.1% ± 0.7% and 3.7% ± 0.7% of the diets of all sampled polar bears, respectively. The proportion of the diet attributed to bearded seals was strongly and positively correlated with the abundance of 22:2Δ7,15 in the adipose tissue of bears in all regions (Fig. 6A). Among polar bears in Baffin Bay, bearded seal consumption and 22:2Δ7,15 concentration (see Fig. 4B) were both very low, but were still significantly correlated ($P = 0.023$). Atlantic walrus biomass accounted for >2% of total mean diet only among polar bears in Foxe Basin (6.9% ± 1.8%). In this population, the abundance of

**Fig. 4.** Abundance of (A) 20:2Δ5,11 and (B) 22:2Δ7,15 (mass percentage of total FA + SE) in adult and harvested (>2.5 years) polar bears. These FA dominated the NMI FA profiles of Atlantic walruses and bearded seals, respectively. Both FA were more abundant in male than in female ($P < 0.001$) bears and both differed significantly by region ($P < 0.001$). Significant sex × region interactions ($P < 0.040$) were driven by low concentrations and little variability among females. Numbers within bars indicate sample sizes in each region.
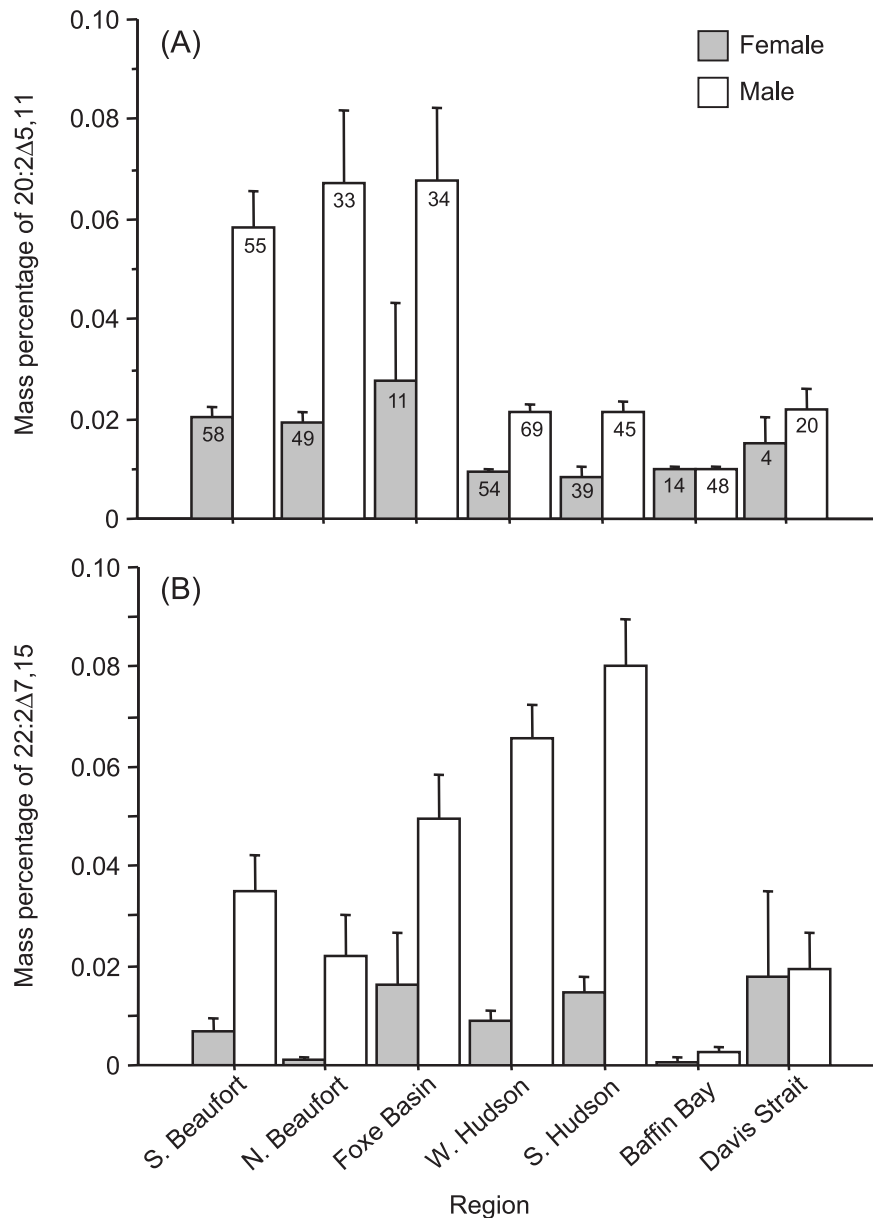


20:2Δ5,11 in polar bear adipose tissue was strongly correlated with Atlantic walrus consumption ($P < 0.001$; Fig. 6B).

## Discussion

Given that NMI FA have only been detected in the tissues of marine molluscs and their predators, we interpreted the presence of these compounds in the blubber of bearded seals, harbour seals, and Atlantic walruses as an indicator of foraging on benthic molluscs. In contrast, harp seals, hooded seals, beluga whales, and narwhals had generally undetectable levels of NMI FA in their blubber. Ringed seals also had relatively low levels of NMI FA, indicating that none

of these species feed extensively on molluscs. These observations are consistent with previous studies on the foraging ecology of arctic marine mammals (reviewed by Pauly et al. 1998).

Although NMI FA in harbour seals rarely accounted for more than 0.1% of total FA, their presence suggests that harbour seals in Western Hudson Bay may occasionally feed on benthic molluscs. The harbour seals that we examined were all sampled near the mouth of the Churchill River in northeastern Manitoba and relatively little is known about their ecology and diet. However, long-term ecological changes in Hudson Bay (Stirling et al. 1999) appear to be having significant effects on predator foraging patterns and reproductive rates (Gaston et al. 2003; Ferguson et al.

**Fig. 5.** Linear regression of $22:2\Delta7,15$ (transformed, mass percentage of total FA) vs. body mass in adult male (○, dashed lines) and female (●, solid line) polar bears handled during mark–recapture studies. Males and females were analyzed separately to account for sex differences in body mass and sample sizes are given for each region. Regression lines indicate significant relationships. When the sexes were pooled, a significant ($P < 0.001$) mass effect was found in each region.
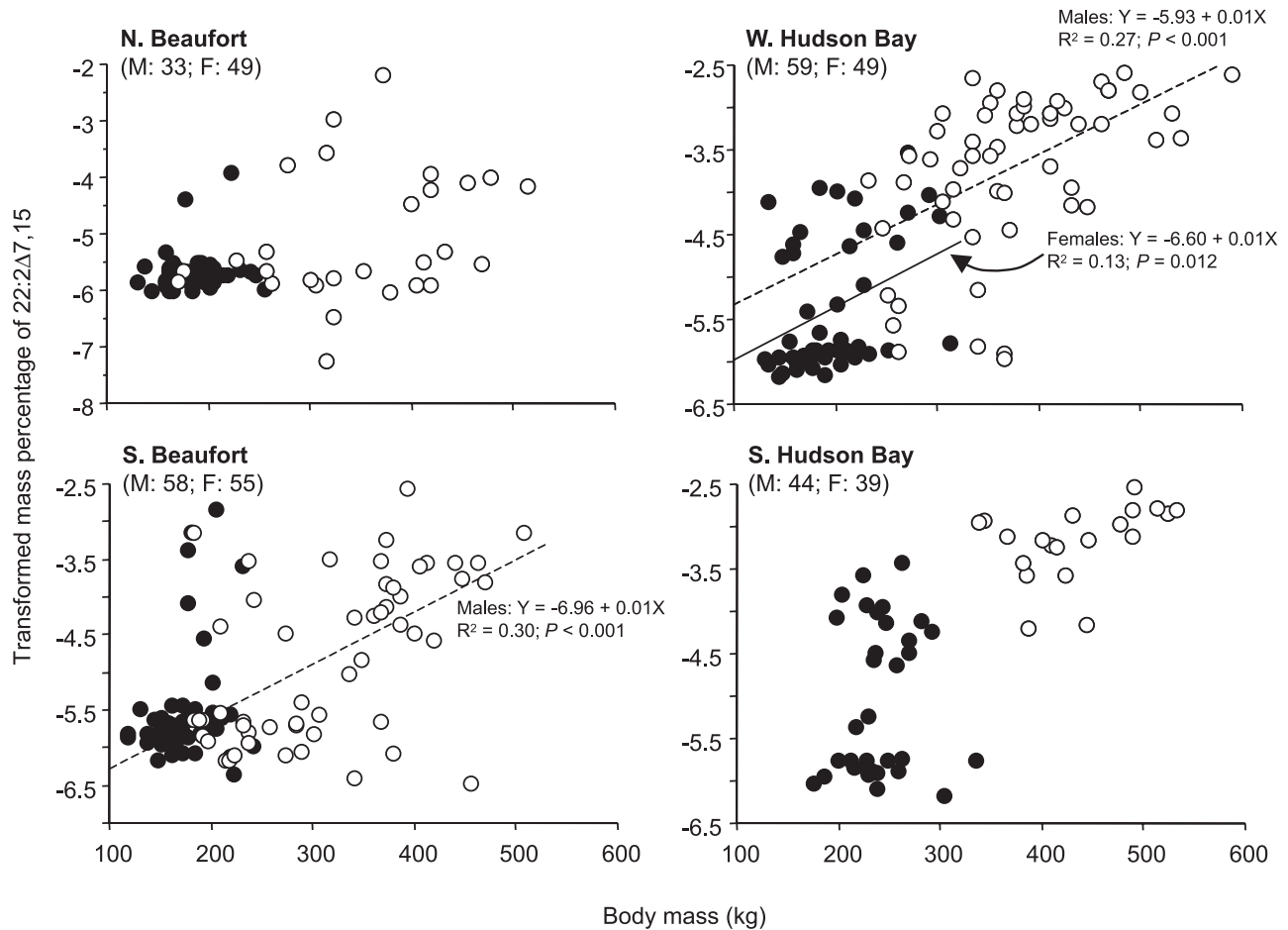


2005). For instance, temperature-related decreases in ice coverage appear to have reduced the availability of arctic cod (*Boreogadus saida* (Lepechin, 1774)) and increased the abundance of capelin (*Mallotus villosus* (Müller, 1776)) in the waters of Hudson Bay (Gaston et al. 2003). The possibility that harbour seals in Western Hudson Bay may be increasing foraging on benthic invertebrates in response to changes in fish availability warrants further investigation.

The NMI FA profiles of Atlantic walruses in Foxe Basin (Fig. 2A) were relatively similar to those reported for Pacific walruses in the Bering Sea (Budge et al. 2007). Walruses in both areas were characterized by high levels of $20:2\Delta5,11$ and moderately high levels of $22:2\Delta7,13$, suggesting relatively little geographic variability in walrus foraging. Stomach content analyses indicate that the diets of walruses in both Foxe Basin and the Bering Sea may be dominated by the bivalves *Mya truncata* L., 1758 and *Serripes groenlandicus* (Mohr, 1786) (Fay 1982; Fisher and Stewart 1997).

The overall NMI FA pattern for bearded seals in the Canadian Arctic was also similar to that of bearded seals in the Bering Sea (Budge et al. 2007). Across the Canadian Arctic, bearded seals were characterized by particularly

high levels of $22:2\Delta7,15$ and relatively low levels of all other NMI FA — a distinctly different pattern than that of walruses. Our data therefore support the conclusions of Budge et al. (2007) who suggested that bearded seals and walruses likely focus on different prey species even though they are both benthic feeders. More data on the FA composition of arctic molluscs should help determine which prey species are most important to each predator.

The NMI FA patterns we observed indicate some regional variability in the diets of bearded seals. For instance, bearded seals in the Beaufort Sea had the lowest level of $22:2\Delta7,15$ and the highest level of $20:2\Delta5,11$ (Fig. 2B). Given that $20:2\Delta5,11$ is most abundant in walrus NMI FA profiles, this pattern suggests that bearded seals in the Beaufort Sea may consume mollusc species more typical of the walrus diet. However, it should be noted that the abundance of this FA in bearded seals of the Beaufort Sea was 40% less than in the Atlantic walruses we sampled. Although little is known about the specific feeding habits of Beaufort Sea bearded seals, stomach-content analyses have demonstrated substantial regional variability in bearded seal diets. For instance, individuals in the Bering and Chukchi seas forage primarily on clams, crabs, and shrimps (Lowry et al.

**Fig. 6.** Correlation between biomarker concentration (mass percentage of total FA) and estimated proportion of (A) bearded seal and (B) Atlantic walrus in the diets of male (○) and female (●) polar bears using QFASA. The concentration of $22:2\Delta7,15$ reflected bearded seal consumption, whereas $20:2\Delta5,11$ was strongly correlated with Atlantic walrus consumption. Polar bears in Baffin Bay (not shown) also had a significant correlation between $22:2\Delta7,15$ and bearded seal consumption (Pearson's correlation, $r = 0.266$, $P = 0.025$), but the values of both variables were very low. Only in Foxe Basin did walrus account for >2% of the total mean diet of polar bears.
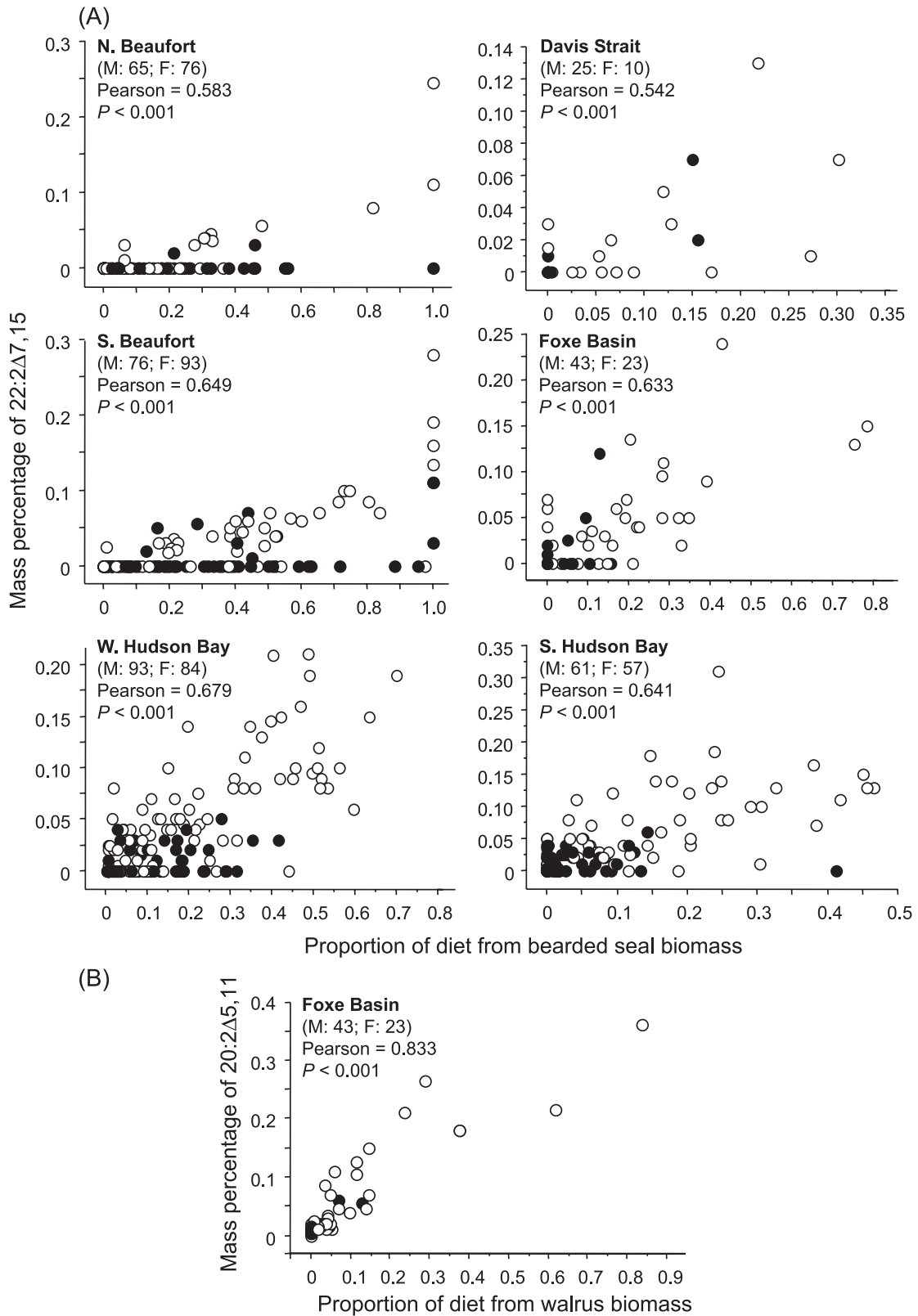
1980), whereas the diets of bearded seals in the High Arctic (Finley and Evans 1983) and the waters around Svalbard, Norway (Hjelset et al. 1999), may be dominated by fish. Despite substantial regional variation in the diets and overall NMI FA profiles of bearded seals, a high level of $22:2\Delta7,15$ appears to be characteristic of this species.

Considering the availability of NMI FA in polar bear prey, we examined the FA composition of polar bear adipose tissue to test two hypotheses: (1) NMI FA are transferred from benthic invertebrates via pinnipeds to polar bears at the top of the food web and (2) individual NMI FA in polar bear fat reflect the consumption of particular prey species. Although polar bears showed absolutely low levels of NMI FA in their adipose tissue (0%–1.4% of total FA), these unusual FA were clearly present and showed significant age-, sex-, and region-specific differences. To our knowledge, this is the first documented evidence of the trophic transfer of individual FA through three trophic levels.

Because mammals, including polar bears, are incapable of endogenously synthesizing NMI FA and given that the molluscs which synthesize and store NMI FA are not part of the polar bear diet, marine mammals are the only potential source of these FA for polar bears. However, it is difficult to make inferences about the dietary origins of FA that are common among prey types without using a quantitative mathematical model (Iverson et al. 2004) even if, as is the case for NMI FA, those FA are limited to only a few prey species. Because $22:2\Delta7,15$ and $20:2\Delta5,11$ are so characteristic of bearded seals and walruses, respectively, we suggest that these individual FA can serve as simple biomarkers for the presence of these prey in polar bear diets. Furthermore, because $22:2\Delta7,15$ and $20:2\Delta5,11$ are directly incorporated into polar bear adipose tissue (i.e., they cannot be synthesized de novo), their relative abundance will reflect the contribution of bearded seal and walrus biomass to polar bear diets.

Considering the dietary origins of NMI FA, our data indicate age-, sex-, region-, and size-specific patterns of polar bear foraging. Specifically, older male polar bears are the most likely to consume prey with elevated blubber NMI FA concentration. We confirmed the relationship between biomarker abundance and prey consumption through QFASA estimates of diet, which independently demonstrated that as bearded seal and Atlantic walrus consumption increased so too did the concentration of $22:2\Delta7,15$ (Fig. 6A) and $20:2\Delta5,11$ (Fig. 6B), respectively. Levels of $22:2\Delta7,15$ therefore indicate that the consumption of bearded seal was greatest among adult and harvested males, followed by adult females, subadults, harvested females, dependent cubs, and independent cubs (Fig. 3A). Although ringed seals tend to be the most common prey item in polar bear diets, other studies have shown that bearded seals represent an important dietary component (Stirling and Archibald 1977; Smith 1980; Iverson et al. 2006). Derocher et al. (2002) concluded that in terms of biomass bearded seals may even be the dominant prey of some polar bears in the Barents Sea. Our results suggest that bearded seals may be too large (up to 350–500 kg) to be routinely killed by juveniles or adult female polar bears, which are roughly half the size of adult males (Derocher and Wiig 2002). Although the differences in $22:2\Delta7,15$ between subadults and dependent and inde-

pendent cubs were not significant, the trends in Fig. 3 are consistent with dependent cubs foraging on the occasional bearded seal scavenged or killed by their mother.

In contrast to $22:2\Delta7,15$, polar bears may obtain $20:2\Delta5,11$ through the consumption of walrus or bearded seal blubber (Fig. 2). However, inferences may still be made about the origins of this FA by considering differences in the regional distribution of the two prey species. For instance, the relatively high levels of $20:2\Delta5,11$ in polar bears in the Beaufort Sea are likely a consequence of bearded seal consumption; bearded seals in this region were enriched in $20:2\Delta5,11$ (Fig. 2B) and walruses in this area are rare (Harington 1966; Kastelein 2002). In Foxe Basin, walruses may be locally abundant and, given the generally higher levels of $20:2\Delta5,11$ in walruses than in bearded seals, the majority of this FA in polar bears in Foxe Basin is likely derived from walrus tissue. Regardless of additional dietary inputs, the strong relationship between $20:2\Delta5,11$ and polar bear diets (Fig. 6B) indicates that this FA accurately reflects walrus consumption in Foxe Basin polar bears. Significant differences in $20:2\Delta5,11$ indicate that within Foxe Basin walruses are consumed most often by adult male polar bears.

Regional differences in prey NMI FA composition may limit the usefulness of these biomarkers to detect spatial differences in polar bear foraging. For instance, variability in the level of $22:2\Delta7,15$ suggests substantial regional variability in the consumption of bearded seal by polar bears (Fig. 4B). However, the relatively low level of $22:2\Delta7,15$ in polar bears in the Beaufort Sea may be at least partly due to the low level of the biomarker in bearded seals in this area. Similarly, high concentrations of $22:2\Delta7,15$ in Hudson Bay bearded seals (Fig. 2B) may have contributed to the high levels observed in Hudson Bay polar bears. We suggest that when considered qualitatively NMI FA biomarkers may be better suited to examining foraging patterns within regions rather than across large geographic ranges. However, the low level of biomarker in Davis Strait polar bears likely reflects the dominant role of harp seals in the diets of these bears (Iverson et al. 2006), regardless of regional differences in bearded seal NMI FA profiles.

Because male polar bears continue to grow after they reach sexual maturity (Derocher and Wiig 2002), the high levels of bearded seal and walrus biomarkers in older male bears suggest that it is their large body size that enables them to hunt large-bodied prey. However, female polar bears may avoid adult males when foraging on the sea ice (Stirling et al. 1993) and differences in bearded seal and walrus consumption may therefore result from differences in access to these prey, rather than their ability to capture them per se. Regression analyses indicated that within the sexes, consumption of bearded seal was significantly related to adult body mass (Fig. 5). Therefore, large body size does appear to improve the ability of polar bears to obtain large bearded seal prey. Although body mass data were not available for bears hunting Atlantic walrus in Foxe Basin, age- and sex-specific trends in $20:2\Delta5,11$ suggest that polar bear body size may also influence walrus consumption. These findings are consistent with the evolutionary theory that the maximum size of available prey has influenced selection for large body size in polar bears (see Stirling and Derocher 1990).

The Arctic is undergoing rapid and significant environmental change (e.g., Parkinson 2000; Comiso 2002; Grebmeier et al. 2006) and climate warming appears to have significantly altered arctic food webs (Gaston et al. 2003; Iverson et al. 2006). Polar bears depend on the sea-ice platform to hunt seals and recent changes in the timing of ice break-up in Western Hudson Bay appear to have contributed to declines in polar bear body condition, natality, and survival (Stirling et al. 1999; Derocher et al. 2004; Stirling and Parkinson 2006). Our data indicate that NMI FA can serve as reliable indicators of foraging in arctic marine mammals. These easily identifiable compounds are directly incorporated from benthically feeding pinniped prey into the adipose tissue of polar bears and, when considered singly, they accurately identify large, adult male bears as the primary predators of bearded seals and Atlantic walruses. Because bearded seals depend on the sea ice to moult and reproduce, reductions in ice coverage may reduce the number of bearded seals available to polar bears. Therefore, in addition to corroborating the results of QFASA, NMI FA biomarkers could be used to detect future shifts in polar bear diets and thereby monitor bottom–up changes in arctic marine food webs.

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