

POLAR BEAR DIETS AND ARCTIC MARINE FOOD WEBS: INSIGHTS FROM FATTY ACID ANALYSIS

GREGORY W. THIEMANN,^{1,3} SARA J. IVERSON,¹ AND IAN STIRLING²

¹Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1 Canada

²Canadian Wildlife Service, 5320 122 St., Edmonton, Alberta T6H 3S5 Canada

Abstract. We used quantitative fatty acid signature analysis (QFASA) to examine the diets of 1738 individual polar bears (*Ursus maritimus*) sampled across the Canadian Arctic over a 30-year span. Polar bear foraging varied over large and small spatial and temporal scales, and between demographic groups. Diets in every subpopulation were dominated by ringed seals (*Phoca hispida*) and, in the eastern Arctic, secondarily by harp seals (*Pagophilus groenlandica*). Beluga whales (*Delphinapterus leucas*) were an important food source for bears in the High Arctic, which is consistent with previous anecdotal reports. Foraging patterns were most similar among neighboring subpopulations with similar prey assemblages, but also differed geographically within Western Hudson Bay. The sexual size dimorphism of polar bears had an important effect on foraging, as large bearded seals (*Erignathus barbatus*) and walrus (*Odobenus rosmarus*) were consumed most often by older, male bears, whereas ringed seals and, where available, harbor seals (*P. vitulina*) were most important to younger age classes. Larger, older bears also had the greatest dietary diversity, apparently because of their ability to include larger-bodied prey. During spring and summer, polar bears in some areas increased predation on migratory harp seals and beluga whales. In Western Hudson Bay, bearded seal consumption declined between 1995 and 2001 for both male and female bears and continued to decline among females up to the most recent sampling (2004). Ringed seal consumption in Western Hudson Bay increased between 1998 and 2001, perhaps in response to increased ringed seal productivity, but was not significantly affected by date of sea-ice breakup. Overall, our data indicate that polar bears are capable of opportunistically altering their foraging to take advantage of locally abundant prey, or to some degree compensating for a decline in a dominant prey species. However, in other areas polar bears are dependent on the availability of ringed and bearded seals. Recent population data suggest that polar bears with the most specialized diets may be most vulnerable to climate-related changes in ice conditions. The results of this large-scale, ecosystem-based study indicate a complex relationship between sea-ice conditions, prey population dynamics, and polar bear foraging.

Key words: Canadian Arctic; climate change; dietary niche; ecosystem structure; feeding ecology; marine food web; marine mammals; polar bears; quantitative fatty acid signature analysis (QFASA); seals; walrus; whales; *Ursus maritimus*.

INTRODUCTION

Apex predators play an important role in determining the structure and functioning of marine ecosystems (e.g., Katona and Whitehead 1988, Estes 1995, Bowen 1997). In the Arctic, polar bears (*Ursus maritimus*) represent a clearly defined fifth trophic level (Hobson and Welch 1992) and feed on a variety of marine-mammal prey (Stirling and McEwan 1975, Stirling and Archibald 1977, Derocher et al. 2002, Iverson et al. 2006). Because of their long life span and wide-ranging distribution, polar bears may provide valuable insights into food-web structure and ecosystem change over multiple temporal and spatial scales.

Manuscript received 27 June 2007; revised 25 February 2008; accepted 13 March 2008. Corresponding Editor: B. J. Danielson.

³ Present address: Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9 Canada. E-mail: thiemann@ualberta.ca

Accurate information on diets is essential to understanding the ecological role of top predators. Studies to date suggest that polar bears feed primarily on ringed seals (*Phoca hispida*), and to a lesser extent on bearded seals (*Erignathus barbatus*; Stirling 1974, Stirling and McEwan 1975, Stirling and Archibald 1977, Smith 1980, Stirling and Øritsland 1995), both of which are available throughout the Canadian Arctic. However, more recent studies by Derocher et al. (2002) and Iverson et al. (2006) have indicated that harp seals (*Pagophilus groenlandica*) may also be important prey in areas where they are available. Opportunistic observations have also identified a wide diversity of apparently less important food items including beluga whales (*Delphinapterus leucas*; Freeman 1973, Heyland and Hey 1976, Lowry et al. 1987, Smith and Sjøre 1990), narwhals (*Monodon monoceros*; Smith and Sjøre 1990), walrus (*Odobenus rosmarus*; Calvert and Stirling 1990), and even conspecifics (Taylor et al. 1985, Amstrup et al. 2006, Stone and

Derocher 2007). Although occasional depredation of caribou (*Rangifer tarandus*) has been documented (Derocher et al. 2000), the nutritional contribution of terrestrially based species appears to be negligible (Ramsay and Hobson 1991, Hobson and Stirling 1997).

Predator foraging strategies may be affected by intrinsic differences in morphology, hunting ability, energy requirements, and reproductive costs. Adult male polar bears are roughly twice the size of adult females (Derocher et al. 2005) and individuals of both sexes continue to grow after reaching sexual maturity (Derocher and Wiig 2002). After mating, females support the entire cost of raising cubs and may endure a denning-related fasting period of more than eight months (Stirling et al. 1977b). Although bears of different age and sex classes show some degree of spatial segregation while foraging on the sea ice (Stirling et al. 1993), little is known about the effects of body size and reproductive costs on polar bear foraging strategies.

Extrinsic factors may also affect predator foraging patterns, and increasing temperatures and declining sea-ice coverage in many parts of the Arctic (e.g., Callaghan and Jonasson 1995, Parkinson 2000, Comiso 2002, 2006) are having significant, yet incompletely understood effects on marine ecosystems (e.g., Gaston et al. 2003, Stirling et al. 2008). Polar bears depend on the sea-ice platform to hunt, and changes in the amount and timing of ice cover may reduce bears' ability to access offshore prey (Stirling et al. 1999, Stirling and Parkinson 2006), as well as affect the distribution, migration patterns, and reproductive success of those prey (Ferguson et al. 2005, Johnston et al. 2005). Earlier summer break-up of the sea ice in Western Hudson Bay over the last 30 years (Stirling et al. 1999, Gough et al. 2004, Gagnon and Gough 2005) is strongly correlated with declines in polar bear body condition, natality, survival, and population size (Stirling and Parkinson 2006, Regehr et al. 2007). Iverson et al. (2006) reported a decrease in ringed seal consumption among Western Hudson Bay polar bears between 1994 and 1998 that correlated with increasingly early spring ice retreat. More recent changes in polar bear diets in Western Hudson Bay, and elsewhere, remain unknown.

Limitations on the synthesis of fatty acids (FA, the primary components of lipids) in mammalian predators result in dietary FA being predictably incorporated into the fat of the consumer (Ackman and Eaton 1966, Iverson et al. 1995, Dalsgaard and St. John 2004). These biochemical restrictions, coupled with the great diversity of FA in marine ecosystems, allow FA to serve as useful indicators of trophic relationships (Brockerhoff et al. 1967, Sargent et al. 1987, Bradshaw et al. 2003). The relative abundance of multiple FA (i.e., the FA profile or "signature") in the adipose-tissue stores of a predator can provide information on diet integrated over a span of weeks to months (e.g., Kirsch et al. 2000, Iverson et al. 2004). Quantitative FA signature analysis (QFASA) uses a multivariate least-squares model to generate

estimates of the relative contributions of different prey species to the FA signatures, and thus the diets, of individual predators (Iverson et al. 2004, 2006, 2007). In this study, we used QFASA to examine the intrinsic and extrinsic factors that influence prey selection among polar bears across the Canadian Arctic over a 30-year time span.

Given regional differences in the abundance and availability of various prey species, we hypothesized that polar bear diets would differ across broad geographic regions. Because polar bears forage over thousands of kilometers and do not defend individual territories (Amstrup et al. 2000), fine-scale (e.g., >1000 km) differences in foraging should be rare. In addition to factors such as prey abundance and availability, we hypothesized that polar bear diets would be affected by age- and sex-specific foraging patterns and that large, adult male bears would be the most likely to capture and consume large-bodied prey (i.e., bearded seals and walrus). Size-related differences in the consumption of beluga whales and narwhals may be less pronounced given that multiple polar bears may scavenge large whale carcasses (Lowry et al. 1987; see Plate 1). Finally, we hypothesized that recent reductions in sea-ice area and extent in many parts of the Canadian Arctic (Stirling and Parkinson 2006) would result in reductions in the consumption of ice-associated seals (i.e., ringed and bearded) and increases in species more associated with open water and seasonal use of pack ice (e.g., harbor seals, *Phoca vitulina*, and harp seals). However, it is also possible that polar bears have a limited ability to capture open-water prey and reductions in sea-ice cover may yield reductions in overall hunting success without dramatic changes in diet composition.

METHODS

Sample collection

A total of 1902 adipose-tissue samples were collected from 1738 individual polar bears handled between 1972 and 2004 (Table 1). Bears were sampled in 10 different Canadian subpopulations (Fig. 1; Lunn et al. 2002): Northern Beaufort Sea, Southern Beaufort Sea, Lancaster Sound, M'Clintock Channel, Gulf of Boothia, Foxe Basin, Western Hudson Bay, Southern Hudson Bay, Baffin Bay, and Davis Strait. Samples were collected from bears of all age and sex classes during mark-recapture studies in Western Hudson Bay, Southern Hudson Bay, Northern Beaufort Sea, and Southern Beaufort Sea. Bears were classified as adults (≥ 5 years), subadults (3–4 years), and cubs (< 3 years). Weaning typically occurs when cubs are 2.5 years old, so some 2-yr-olds were captured as independent cubs, whereas other bears of the same age were still associated with their mothers. Because association with its mother will likely influence a bear's diet (Stirling and Latour 1978), bears under three years of age were further classified as either "dependent" or "independent" cubs. All free-ranging polar bears were located from a Bell 206B

TABLE 1. Distribution of all samples collected from 1738 different polar bear adults (≥ 5 yr old), subadults (3–4 yr old), and cubs (< 3 yr old) across the Canadian Arctic from 1972 to 2004.

Subpopulation	Total no. samples	Adult		Harvested (≥ 2.5 yr)		Subadult		Independent cub		Dependent cub	
		F	M	F	M	F	M	F	M	F	M
Northern Beaufort Sea	181	57	48	4	5	4	11	3	1	23	25
Southern Beaufort Sea	217	75	70	0	2	18	15	3	2	18	14
Lancaster Sound	94	11	43	1	8	5	21	1	4	0	0
M'Clintock Channel	15	3	9	0	1	0	1	1	0	0	0
Gulf of Boothia	69	10	24	4	5	8	13	0	4	0	1
Foxe Basin	109	13	38	5	18	13	18	1	3	0	0
Western Hudson Bay	755	257	226	15	22	21	39	21	19	64	71
Southern Hudson Bay	195	78	66	1	1	22	22	3	1	0	1
Baffin Bay	101	9	52	6	10	6	16	0	2	0	0
Davis Strait	166	28	57	12	16	23	22	3	5	0	0
Total	1902	541	633	48	88	120	178	36	41	105	112

Notes: All samples from independent-age bears (≥ 2.5 years, excluding those from M'Clintock Channel) were used to examine long-term temporal changes in polar bear diets. Samples collected between 1999 and 2004 were used to examine demographic, regional, and seasonal differences in diets. "Harvested (≥ 2.5 yr)" bears were the subset of harvested bears that were of unknown age but were independent of their mothers and therefore assumed to be at least 2.5 years old. F = female, M = male. See Fig. 1 for locations.

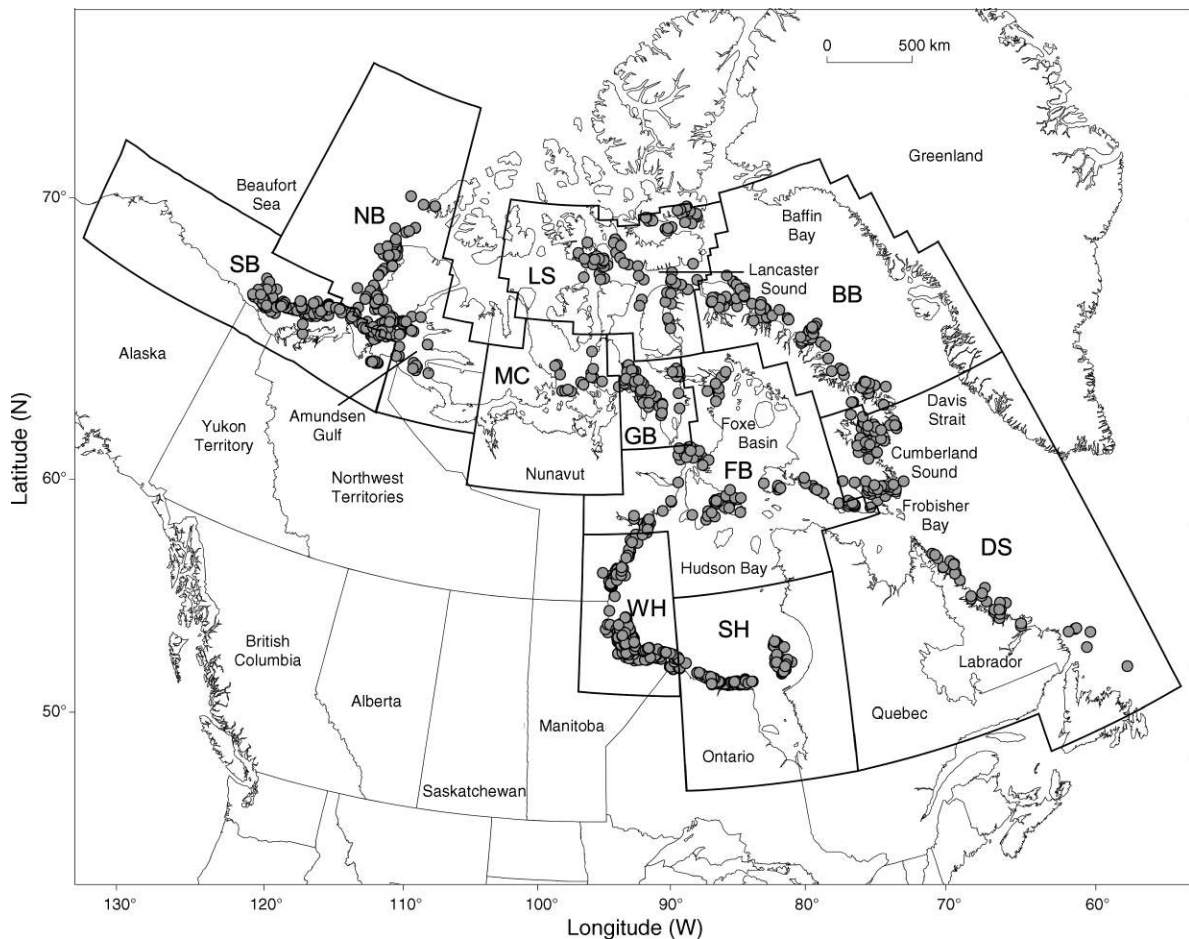


FIG. 1. Locations of all samples ($n = 1902$) collected from 1738 individual polar bears between 1972 and 2004 in 10 Canadian polar bear subpopulations as defined by Lunn et al. (2002): Northern Beaufort Sea (NB), Southern Beaufort Sea (SB), Lancaster Sound (LS), M'Clintock Channel (MC), Gulf of Boothia (GB), Foxe Basin (FB), Western Hudson Bay (WH), Southern Hudson Bay (SH), Baffin Bay (BB), and Davis Strait (DS). See Table 1 for sample sizes from the different regional subpopulations and age classes.



PLATE 1. A young adult polar bear scavenges the remains of a sperm whale on the coast of Svalbard, Norway. Photo credit: I. Stirling.

JetRanger helicopter and immobilized with a combination of tiletamine hydrochloride and zolazepam hydrochloride (Telazol; Fort Dodge Laboratories, Fort Dodge, Iowa, USA) following standard chemical immobilization protocols (Stirling et al. 1989).

Adipose-tissue samples were collected from immobilized bears using a 6 mm biopsy punch and consisted of a full-layer core from skin to muscle, taken ~15 cm lateral to the base of the tail (Ramsay et al. 1992, Thiemann et al. 2006). At the time of first capture, each animal was assigned a unique identification number that was permanently tattooed on the inside of each upper lip and engraved on plastic tags attached to each ear. A vestigial premolar tooth was extracted from independent bears and their ages determined by counting growth-layer groups in the cementum (Calvert and Ramsay 1998). All immobilization and live-capture procedures were reviewed and approved annually by the Animal Care Committee of the Canadian Wildlife Service, Prairie and Northern Region, Edmonton, Alberta, Canada.

In addition to live-captured bears, adipose-tissue samples were collected from bears harvested by Inuit subsistence hunters in all 10 subpopulations. Although the ages of most harvested bears were determined by sectioning a tooth, age data for some bears ($n = 136$ individuals) were unavailable (see Table 1). Because it is illegal to hunt polar bears that are still associated with their mothers, it was assumed that all harvested bears

were at least 2.5 years old. Bears in this group of unknown age (but ≥ 2.5 yr) are referred to in the *Results* as “harvested” bears and they could include independent cubs, subadults, and adults. Considering the age distribution of all known-age hunter-killed bears (61% adult), these samples likely represented mainly adults. Large samples ($\sim 8 \times 8$ cm) extending through the depth of the subcutaneous adipose layer and including a portion of attached muscle were collected from each hunted bear, wrapped in foil, and stored frozen until analysis. The vast majority of these samples (96%) were taken from the rump of the animal, but in some cases, fat was obtained from bacula that were submitted for sex verification of harvested bears. Because the fat deposits on the baculum and rump of an individual bear have identical fatty acid (FA) compositions (Thiemann et al. 2006), all samples were treated equally. In the laboratory 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). We found no differences in the data produced from large, hunter-collected adipose samples and the biopsies collected from live, anesthetized bears.

Samples from all years ($n = 1902$ samples) were used to examine long-term temporal trends in polar bear FA signatures and diets. Iverson et al. (2006) presented preliminary data from polar bears sampled between 1972 and 1998 in the Beaufort Sea, Western Hudson Bay, and Davis Strait. The current study reanalyzed

those samples (i.e., new diet estimates were generated) using a more complete modeling data set (see *QFASA modeling*, below) and greatly expanded the temporal, spatial, and intraspecific scope of the investigation. To control for longer-term temporal trends, regional and demographic differences were tested using a single sample (the most recent) from each bear handled between 1999 and 2004 ($n = 1488$ bears). Seasonal differences could only be tested in subpopulations where samples were collected in more than one season; to again control for long-term temporal effects, these analyses were also limited to samples collected after 1998, but included some individual bears sampled in multiple seasons and/or years ($n = 668$ bears). The vast majority of these samples were collected either in spring (February–May; $n = 321$ samples) or fall (August–November; $n = 288$ samples) and seasonal comparisons were therefore made between spring–summer (February–July), and fall–winter (August–January). Bears ≥ 2.5 years ($n = 1670$ bears; Appendix A) were used to examine interannual differences in polar bear FA signatures and diets. Because different age classes were sampled in different regions and seasons, independent-age (≥ 2.5 yr) bears were also used to examine regional and seasonal variability.

Laboratory analysis

Lipid was quantitatively extracted from each adipose-tissue sample according to Iverson et al. (2001) and FA methyl esters (FAME) were prepared using H_2SO_4 as a catalyst (Thiemann et al. 2004). Duplicate analyses and identification of FAME were performed using temperature-programmed gas–liquid chromatography according to Iverson et al. (1997, 2002) and Budge et al. (2002, 2006). 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 \times 0.25 mm inner diameter) coated with 50% cyanopropyl polysiloxane (0.25- μ m film thickness) (DB-23; Agilent Technologies, Palo Alto, California, USA). FA data are expressed as the mass percentage of total FA ± 1 standard error of the mean (SEM). Individual FA are referred to by the shorthand nomenclature of carbon-chain length:number of double bonds, and position of the first double bond relative to the terminal methyl group.

Regional differences in polar bear FA signatures were tested using a combination of multivariate analysis of variance (MANOVA), hierarchical cluster analysis, and discriminant analysis (SPSS 2000). MANOVA were also used to examine temporal and demographic differences in polar bear FA signatures. The values of 17 of the most abundant and variable FA (Appendix B) were transformed to improve normality by calculating the log of the ratio of each FA to 18:0 (Budge et al. 2002, Iverson et al. 2002). Because the sample size of any group must exceed the number of response variables (Stevens 1986, Legendre and Legendre 1998), only

groups with at least 18 polar bears were examined by discriminant analysis or MANOVA. In contrast, because hierarchical cluster analysis utilizes average FA signatures, all FA can be used.

QFASA modeling

A quantitative estimate of diet was generated for each polar bear sample using the QFASA (quantitative FA signature analysis) model developed by Iverson et al. (2004). Briefly, this process involves first determining the average FA signature of each potential prey type as presented in Thiemann et al. (2008). A combination of multivariate statistical analyses (Thiemann et al. 2008) and simulation studies (described below) are used to ensure that the various prey types are distinct enough to be resolved in the estimated predator diet. A multivariate least-squares model then determines the combination of average prey signatures that most closely matches the observed predator signature, after accounting for FA metabolism within the predator (see below). The estimated combination reflects the contribution of each prey type's FA to the overall signature, and thus the diet, of the predator. In this way, a quantitative diet estimate is generated for each individual polar bear, based on the biochemical assimilation of more than 30 dietary components (FA). Quantitative diet estimates can also be generated from stable-isotope data utilizing a statistical mixing model (e.g., Bentzen et al. 2007). However, because it incorporates a far greater amount of dietary information (i.e., >30 FA compared to two stable-isotope ratios), QFASA can potentially yield more precise estimates of predator diets.

Marine-mammal blubber samples were used to determine prey FA composition. A total of 843 blubber samples from the following prey species were collected across the Canadian Arctic and analyzed as described above: ringed seals, bearded seals, harp seals, hooded seals (*Cystophora cristata*), harbor seals, walruses, beluga whales, and narwhals (see Thiemann 2006, Thiemann et al. 2007b, 2008). Samples were collected from animals of all age classes shot nonselectively by Inuit hunters or sampled during the course of other research projects. Blubber fat content is similar across species and we therefore did not need to account for differences in prey lipid content (see Iverson et al. 2004).

Because average prey signatures were used in the modeling, single diet estimates did not incorporate the FA variability within a prey species. To capture this variability, we used the bootstrapping procedure described in Iverson et al. (2004). Briefly, prey samples were randomly selected from the database and used to generate new prey means and predator diet estimates. This sampling-with-replacement procedure was performed 1000 times and the results used to calculate a within-predator standard error of each diet estimate (Iverson et al. 2004). For a group of bears, the average within-bear standard error ($SE_{w(j)}$) for each prey type (j) was calculated as follows:

$$SE_{w(j)} = \sqrt{\left(\sum_{i=1}^n SE_{w(ji)}^2\right)/n}$$

where $SE_{w(ji)}$ is the within-bear standard error for prey type (j) for individual bear (i) using the bootstrapping procedure, and n is the number of bears (see Beck et al. 2007). Total SE for each prey type (j) was calculated using both the within- and between-bear standard error as follows:

$$\text{Total } SE_j = \sqrt{(SE_{w(j)}^2 + SE_{b(j)}^2)/n}$$

where $SE_{b(j)}$ is the standard error of the mean percentage of the diet accounted for by prey type (j) between individual polar bears (Beck et al. 2007).

Bears in each region were modeled on the prey species present in that region and, where possible, using prey samples collected in that area (Appendix C). Where necessary, we modeled bear diets using prey samples collected outside the subpopulation region. Although prey FA signatures may vary spatially, this variability is small compared to differences between species (Thiemann et al. 2008). We used simulation studies (Iverson et al. 2004, 2006) to test the ability of the QFASA model to distinguish between different polar bear prey types. Following the methods of Iverson et al. (2004), the first step in this approach was to arbitrarily define the hypothetical composition of polar bear diets in a given region (e.g., 75% ringed seal, 25% bearded seal). The prey data set for that region was then randomly split into two equal-sized groups: a simulation group and a modeling group. The simulation group was used to construct a “pseudo-bear” signature using the diet proportions specified in the first step. The modeling group was then used to estimate the “diet” of this pseudo bear. The creation of the pseudo-bear and subsequent modeling was repeated 1000 times. The results of the simulation provide an indication of both the accuracy and precision with which the diet can be estimated using a given prey data set.

Bears were modeled using a set of 31 FA (Appendix B) that was based on Iverson et al.’s (2004) “dietary” set of FA. These FA are obtained primarily or exclusively through diet. However, not all ingested FA are directly incorporated into adipose stores. Rather, some FA are modified or utilized prior to deposition while others, in addition to coming from dietary sources, are synthesized endogenously from non-lipid precursors. Nevertheless, ingested FA are incorporated into predator fat stores in predictable ways, and calibration coefficients have been developed to account for predator metabolism (Iverson et al. 2004, 2007). To generate calibration coefficients for polar bears we used another terrestrial carnivore, the mink (*Mustela vison*), as a model. By comparing the adipose-tissue composition of captive mink ($n = 37$ individuals) with the FA composition of their diet (either poultry, herring, or herring supplemented with seal oil) we generated calibration coefficients suitable for a

terrestrial carnivore feeding on marine-based prey (Appendix D; Thiemann 2006).

Some prey types did not appear in the QFASA estimates of some bears and diet data were therefore not normally distributed. To account for this, we used randomization–permutation analyses (e.g., Efron and Tibshirani 1998, Good 2000, Anderson 2001, Beck et al. 2007) to examine spatial, temporal, and demographic differences in polar bear diet estimates. In this procedure, diets were tested via MANOVA after randomly permuting the factor levels 10000 times. This random permutation generated a reference distribution (rather than a more typically used theory distribution) against which the MANOVA test statistic was compared. Post hoc analyses were similarly performed using multivariate and univariate t tests. Two-way MANOVA were used to test for age- and sex-specific differences in polar bears diets, as well as to factor out sex effects when comparing polar bear diets across areas, seasons, or years. The relationship between specific prey consumption and timing of sea-ice breakup in Western Hudson Bay was examined using simple linear regression. The dietary-niche breadth of polar bears was calculated using the Shannon-Wiener Index (H' ; Krebs 1999):

$$H' = -\sum_s^j p_j \ln p_j$$

where p_j is the proportion of prey species j in the diet and S is the total number of prey species consumed by all individuals. Two-way ANOVA was used to examine age and sex effects on dietary diversity. Two-way ANOVA was also used to account for sex differences among independent-age bears while testing for location, season, and year effects on diet diversity.

RESULTS

Polar bear FA signatures

Across all 10 subpopulations of Canadian Arctic polar bears and across all years, 690 samples (485 males, 205 females) were collected from harvested polar bears and another 1212 samples (567 males, 645 females) were collected during mark–recapture studies. Approximately 65 fatty acids (FA) were routinely identified in polar bear fat samples; those that accounted for >0.2% of all FA are listed by subpopulation in Appendix B.

The FA composition of polar bear adipose tissue varied significantly across regions (MANOVA: Wilks’ $\lambda = 0.006$, $P < 0.001$). Hierarchical cluster analysis (Fig. 2a) indicated that adjacent subpopulations tended to have the most similar FA signatures, whereas those separated by greater distances or significant land masses had more distinct signatures. Consistent with these results, discriminant analysis classified 80.9% of original polar bear samples and 79.8% of cross-validated samples to their correct region (Fig. 2b). The first two discriminant functions accounted for 88% of total variance.

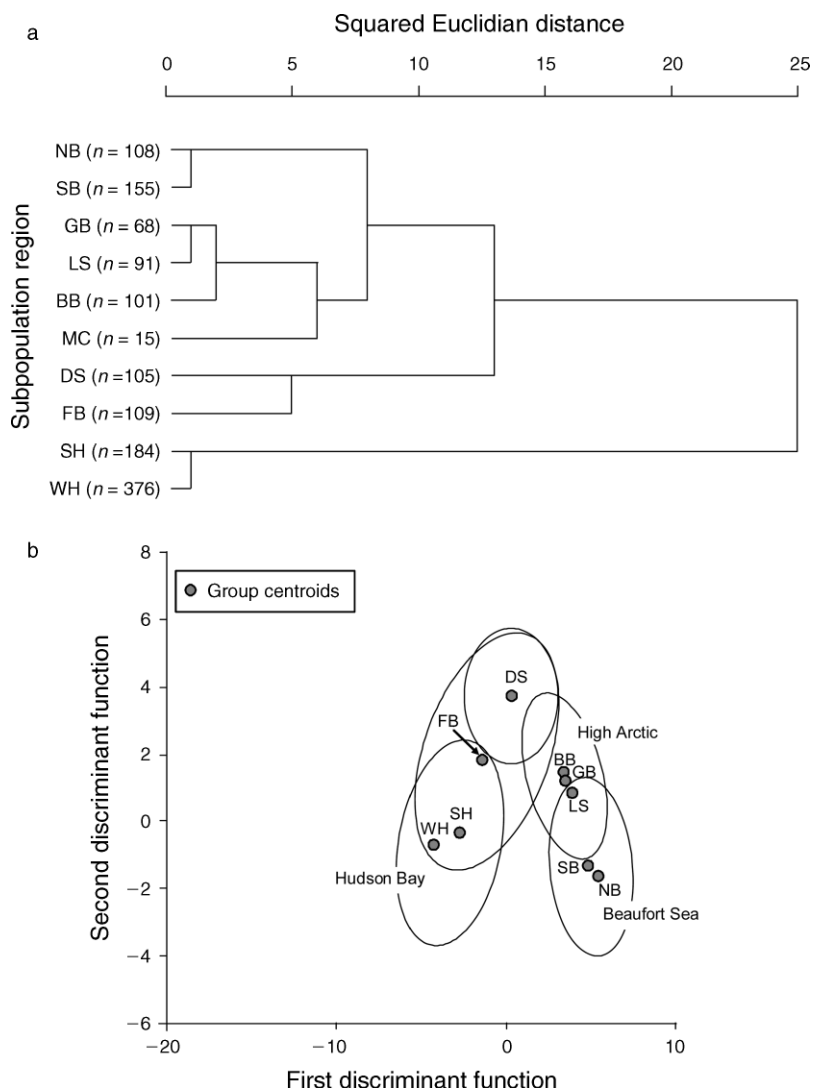


FIG. 2. Results of fatty acid (FA) analysis. (a) Hierarchical cluster analysis of average FA signatures of independent-age (≥ 2.5 years) polar bears in 10 Canadian subpopulations. Clusters were formed based on squared Euclidean distance, using 64 FAs and the between-groups linkage method, and indicated that differences in FA signatures tended to increase with geographic distance. (b) Discriminant analysis of independent-age polar bears in nine Canadian subpopulations, using the 17 most abundant and variable FAs (Appendix B). The first and second discriminant functions accounted for 88% of total variance. Discriminant analysis classified 80.9% of original grouped cases and 79.8% of cross-validated grouped cases to their correct region. Ellipses represent 95% data-point clouds. See Fig. 1 for key to abbreviations of subpopulation regions.

When examined within each region, age had a significant effect ($P < 0.050$) on polar bear FA signatures in every subpopulation except Lancaster Sound, Gulf of Boothia, and Baffin Bay. Sex had a similarly widespread effect, with significant differences ($P < 0.040$) between males and females in all regions except Lancaster Sound, Baffin Bay, and Davis Strait. Too few bears were sampled in M'Clintock Channel to examine demographic differences in FA signatures.

Polar bear FA profiles differed between spring–summer and fall–winter ($P < 0.020$) within six regional subpopulations: Lancaster Sound, Gulf of Boothia, Foxe Basin, Southern Hudson Bay, Baffin Bay, and Davis Strait.

Significant interannual differences were found in every region ($P < 0.010$) analyzed. Again, too few samples were collected in M'Clintock Channel to examine trends.

Simulation studies

In all 10 subpopulations examined in this study, diet simulations demonstrated that prey species could be reliably differentiated and quantified in the quantitative fatty acid signature analysis (QFASA) model (e.g., Fig. 3). To explore the possibility that polar bears target young prey (Stirling and Archibald 1977), we ran simulations on prey species split by age class. The accuracy and precision of these diet simulations were

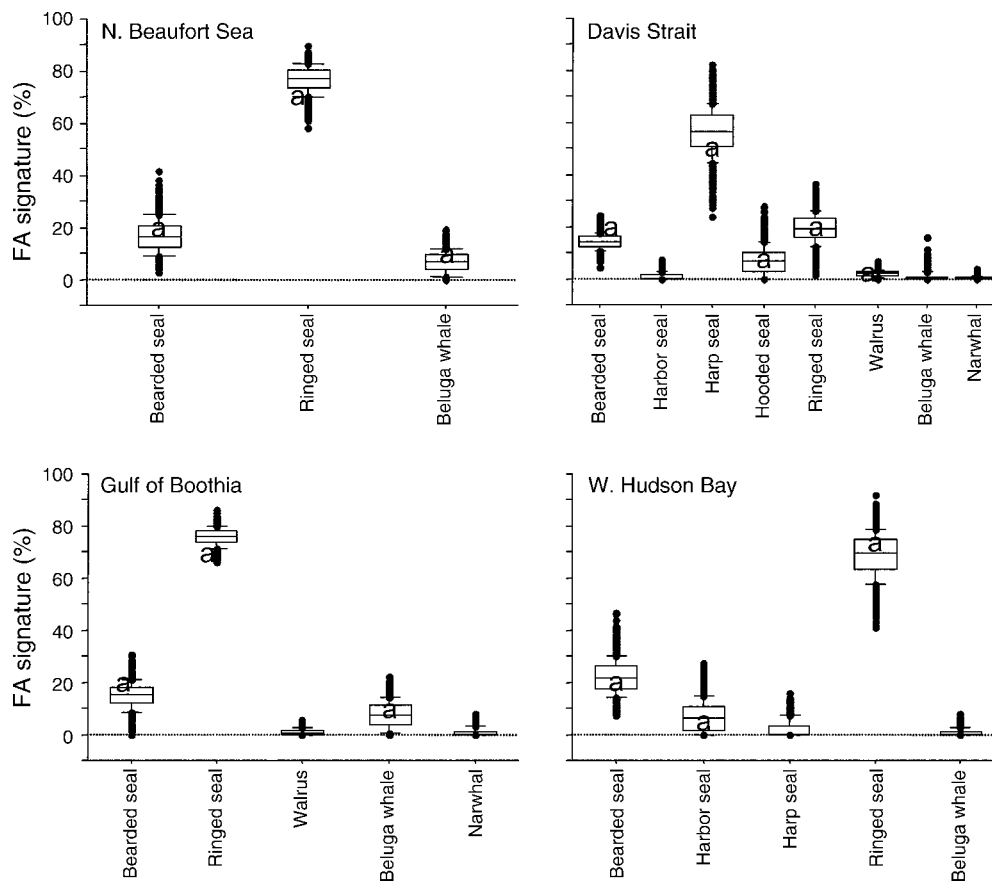


FIG. 3. Results of simulation studies for Northern Beaufort Sea, Davis Strait, Gulf of Boothia, and Western Hudson Bay prey data sets. Results are presented as boxplots showing the 25th, median, and 75th percentiles of the 1000 diet estimates. Solid circles represent outliers. Simulated diet composition is indicated by “a” and was designated for each region as follows: N. Beaufort, 20% bearded seal, 70% ringed seal, and 10% beluga whale; Davis Strait, 20% bearded seal, 0% harbor seal, 50% harp seal, 8% hooded seal, 20% ringed seal, 2% walrus, 0% beluga, and 0% narwhal; Gulf of Boothia, 20% bearded seal, 70% ringed seal, 0% walrus, 10% beluga, and 0% narwhal; Western Hudson Bay, 20% bearded seal, 5% harbor seal, 0% harp seal, 75% ringed seal, and 0% beluga.

reduced and indicated that age-specific variability in prey FA signatures was not large enough to resolve age differences in the prey consumed. Not surprisingly, when modeling was performed using prey split by age class, polar bear diets were often entirely allocated to a single age category. However, the species composition of estimated diets was the same regardless of whether prey were split by age. Therefore, final modeling was performed on prey samples grouped by species alone.

Estimation of polar bear diets

Fig. 4 illustrates the estimated relative contributions of different prey species' biomass to polar bear diets in each subpopulation region. Because the prey species consumed by polar bears vary greatly in size, these data do not necessarily reflect the relative number of prey items consumed. We scaled FA contributions by prey body mass (relative to the smallest prey, ringed seals) to estimate the relative number of individuals of each species consumed (Fig. 5; see Iverson et al. 2006). The

following average body-mass values were used for scaling: ringed seal (65 kg), bearded seal (300 kg), harbor seal (87 kg), harp seal (110 kg), hooded seal (250 kg), walrus (1040 kg), beluga whale (1500 kg), and narwhal (1300 kg). These rescaled data should be considered cautiously as the conversion factors assumed that the entire blubber layer of each prey item was consumed and that blubber mass scaled equally across prey age classes and species. Considering the large body sizes of bearded seals, walruses, beluga whales, and narwhals it is unlikely that the entire blubber layer of these prey would be consumed by a single bear. Therefore, the best estimate for the relative number of prey consumed likely lies somewhere between the FA contribution to fat stores and the rescaled estimate (i.e., Figs 4 and 5). Henceforth, “diets” are primarily presented as percentage contribution of prey fat to polar bear FA signatures. However, it is important to keep in mind that consumption of a large prey will contribute proportionately more to polar bear FA signatures than will a small-bodied prey.

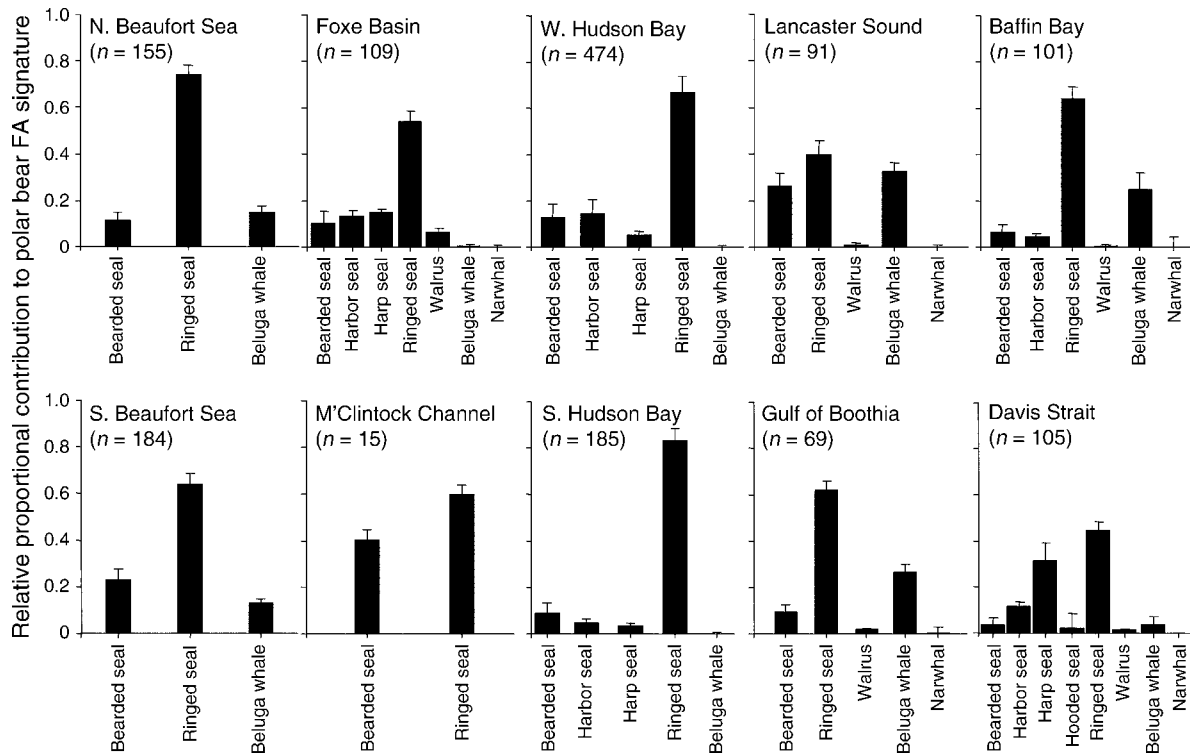


FIG. 4. Diet composition, by subpopulation region, of all polar bears sampled ($n = 1488$ bears) between 1999 and 2004. Data represent the contribution of fat from each prey type to polar bear FA signatures and therefore reflect the contribution of each species' biomass to polar bear diets. Bears in each region were modeled using the prey types available in that area. Data are means + total SE, which incorporates bootstrapped, within-bear variability in QFASA (quantitative FA signature analysis) estimates as well as between-bear variability in diets (see *Methods: QFASA modeling*).

Regional differences in polar bear diets

Although ringed seals were important prey in every region (Fig. 4), the results of QFASA modeling indicated substantial regional variability in polar bear foraging. In Southern Hudson Bay, ringed seal comprised $83\% \pm 5\%$ (total SEM; see *Methods: QFASA modeling*, above) of polar bear FA signatures, whereas bears in Lancaster Sound obtained only $40\% \pm 6\%$ of their ingested biomass from ringed seal. In terms of the relative number of prey animals consumed, ringed seals accounted for $>50\%$ of prey consumed in every region (Fig. 5).

Bearded seal biomass appeared in the diets of bears in all subpopulations and was most prevalent in M'Clintock Channel ($40\% \pm 4\%$) and Lancaster Sound ($26\% \pm 5\%$; Fig. 4). The sometimes-large contribution of bearded seal to polar bear diets was likely related to the large size of these prey, as relatively few animals would need to be killed to account for this level of biomass consumption (Fig. 5). Harp seal was abundant in the diet of bears in Davis Strait ($32\% \pm 8\%$) whereas predation on harbor seal was highest in Western Hudson Bay ($15\% \pm 6\%$). Bears in Foxe Basin fed on the largest proportion of walrus ($7\% \pm 1\%$). In Lancaster Sound, Baffin Bay, and Gulf of Boothia, polar bears derived 25–33% of their ingested biomass

from beluga whale. Narwhal appeared in the diets of bears in some regions, but the very small estimates were generally exceeded by the total standard error.

Although polar bears in the High Arctic may have access to harp seals for at least part of the year, we were unable to collect samples from this species in the High Arctic. When bears in Baffin Bay, Lancaster Sound, and the Gulf of Boothia were modeled using harp seals collected in Davis Strait, the QFASA model performed poorly and was unable to distinguish harp seal from other prey types—including ringed seal, bearded seal, and beluga whale. Consequently, the diets of polar bears in Baffin Bay, Lancaster Sound, and the Gulf of Boothia were estimated without harp seals in the prey library.

Shannon-Wiener Index values indicated that polar bear diets were most diverse in Lancaster Sound ($H' = 0.881$), Foxe Basin ($H' = 0.815$), and Davis Strait ($H' = 0.802$). Bears in Southern Hudson Bay ($H' = 0.479$) and Northern Beaufort Sea ($H' = 0.477$) had the least diverse diets, despite potentially greater prey choice than bears in some other areas.

Polar bear diets also differed across relatively fine spatial scales. After accounting for differences between the sexes, ringed seal was more abundant in the diets of bears in the Northern Beaufort Sea (two-way MANOVA, $P = 0.007$) than the Southern Beaufort, whereas

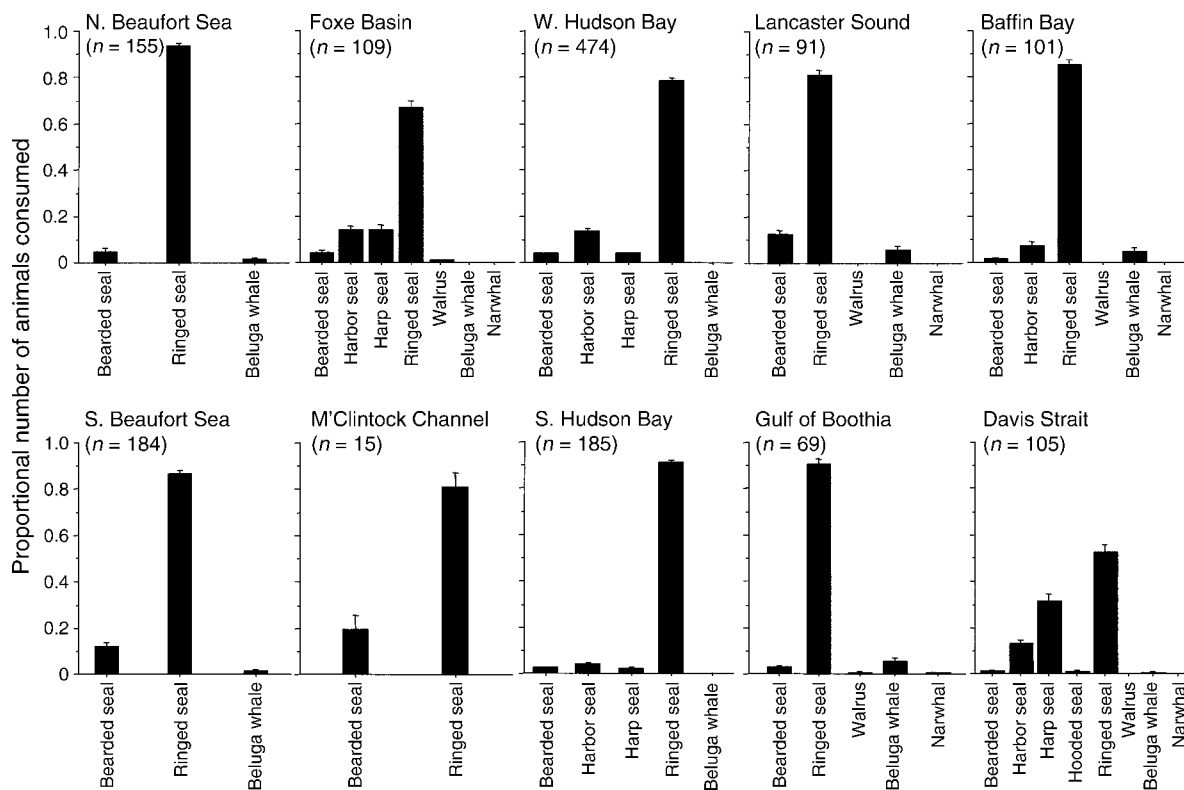


FIG. 5. Diet composition of the same polar bears presented in Fig. 4 ($n = 1488$ bears sampled), rescaled by prey body size (wet body mass) to estimate the relative number of prey items consumed (see *Results: Estimates of polar bear diets*; see Iverson et al. 2006). Data are means + SE.

bears in the Southern Beaufort consumed more bearded seal ($P = 0.004$; Fig. 6a). Among the three High Arctic subpopulations in Fig. 6 (Gulf of Boothia, Baffin Bay, and Lancaster Sound), bearded seal and beluga whale consumption was highest in Lancaster Sound ($P < 0.050$; Fig. 6b), whereas bears in Gulf of Boothia and Baffin Bay consumed the most ringed seal ($P < 0.001$). Bears in the Gulf of Boothia consumed the most walrus ($P < 0.001$).

In the Hudson Bay–Foxe Basin area, polar bear diets were affected by location ($P < 0.001$) and by a sex \times location interaction ($P < 0.001$; Fig. 6c). Bears sampled along the northeastern coast of Manitoba (i.e., south of 60° N) consumed more bearded seal than bears in Foxe Basin ($P = 0.004$), Southern Hudson Bay ($P < 0.001$), or even bears of the same subpopulation sampled north of 60° N (i.e., Nunavut; $P = 0.004$). However, this regional trend was driven almost entirely by male bears; females in all areas consumed relatively little bearded seal biomass. Harbor seal was consumed most often by polar bears in northwestern Hudson Bay ($P < 0.001$) whereas bears in Foxe Basin and northwestern Hudson Bay consumed the most harp seal ($P < 0.001$). Ringed seal consumption was greatest in Southern Hudson Bay ($P < 0.001$). In contrast to these fine-scale differences, within the Baffin Bay region, there were no significant differences in prey consumption between polar bears

sampled north or south of 70° N ($P = 0.091$). Within the Davis Strait region, diets did not differ between bears sampled in Cumberland Sound, Frobisher Bay, or off the coast of Labrador ($P = 0.078$).

Demographic differences in polar bear diets

Two-way MANOVA on polar bear diets showed significant age- and/or sex-specific differences within every subpopulation except Gulf of Boothia and Lancaster Sound. Too few samples were collected in M'Clintock Channel to allow demographic comparisons. In the Northern Beaufort Sea, ringed seal consumption was similar among all age groups, but dependent cubs and adults consumed the most beluga whale ($P < 0.010$; Fig. 7a). In the Southern Beaufort Sea, female bears consumed more ringed seal ($P = 0.003$) and less bearded seal ($P = 0.013$) than male bears (Fig. 7b). Diets in Foxe Basin and Western Hudson Bay were both affected by age ($P < 0.030$) and sex ($P < 0.010$, Fig. 8a, b) and in the case of Western Hudson Bay, by a significant age \times sex interaction ($P < 0.001$). In both regions, consumption of bearded seal was greatest among older males and lowest among independent female cubs. Harbor seal was generally consumed most often by females and young males and, in Western Hudson Bay, ringed seal consumption by male bears declined with age. Across both sexes, walrus consump-

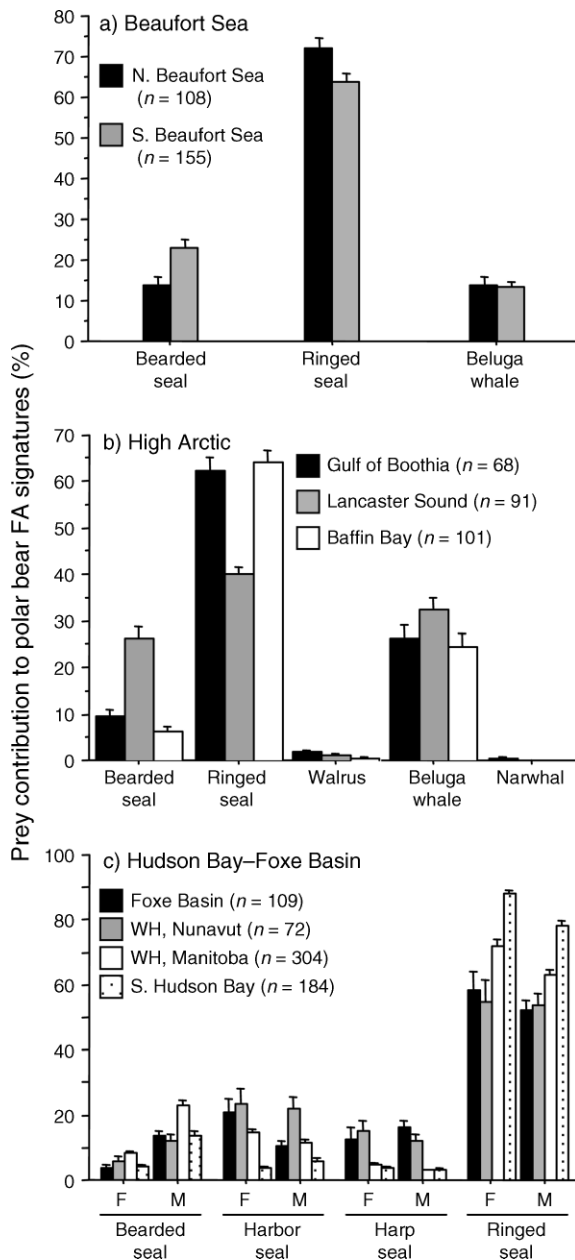


FIG. 6. Geographic differences in the diet composition of independent-age polar bears (≥ 2.5 yr) in three large regions of the Canadian Arctic. Data from males (M) and females (F) are presented separately in areas with a sex \times region interaction (panel c). Data here and in Figs. 7–10 reflect the mean (\pm SE) contribution of each species' fat to polar bear FA signatures and were compared by permutation MANOVA within each region. Western Hudson Bay (WH) samples were separated into those sampled north (Nunavut) or south (Manitoba) of 60° N. Significant spatial differences in diets were present in all three areas ($P < 0.010$), with significant region \times sex interactions in Hudson Bay-Foxe Basin ($P = 0.001$).

tion in Foxe Basin increased with age ($P = 0.015$). In Southern Hudson Bay, significant age ($P = 0.002$), sex ($P < 0.001$), and interactive effects ($P = 0.013$) were driven by an age-specific increase in bearded seal and decrease in ringed seal in the diets of male polar bears (Fig. 8c).

In Baffin Bay and Davis Strait, diets were affected by age (Baffin Bay, $P = 0.039$; Davis Strait, $P = 0.001$) but not by sex (Baffin Bay, $P = 0.432$; Davis Strait, $P = 0.638$; Fig. 9). In Davis Strait the relative consumption of bearded seal, harp seal, hooded seal, and beluga whale all increased with age ($P < 0.040$), whereas ringed seal consumption declined ($P < 0.040$). In Baffin Bay, harbor seal consumption was greatest among subadults and independent cubs ($P < 0.050$).

Across the Canadian Arctic, diet diversity differed by sex (two-way ANOVA: $P < 0.001$) and age class ($P = 0.002$). Dietary breadth was higher among males ($H' = 0.706$) than females ($H' = 0.594$) and higher among harvested (≥ 2.5 yr old) bears ($H' = 0.739$) than among adults ($H' = 0.663$) or juveniles ($H' = 0.623$). Within subpopulations, diversity differed between the sexes in Foxe Basin ($P = 0.026$) and between sex and age classes in Western Hudson Bay (age, $P < 0.001$; sex, $P = 0.001$) and Southern Hudson Bay (age, $P < 0.001$; sex, $P = 0.001$). In all three regions diet diversity was higher

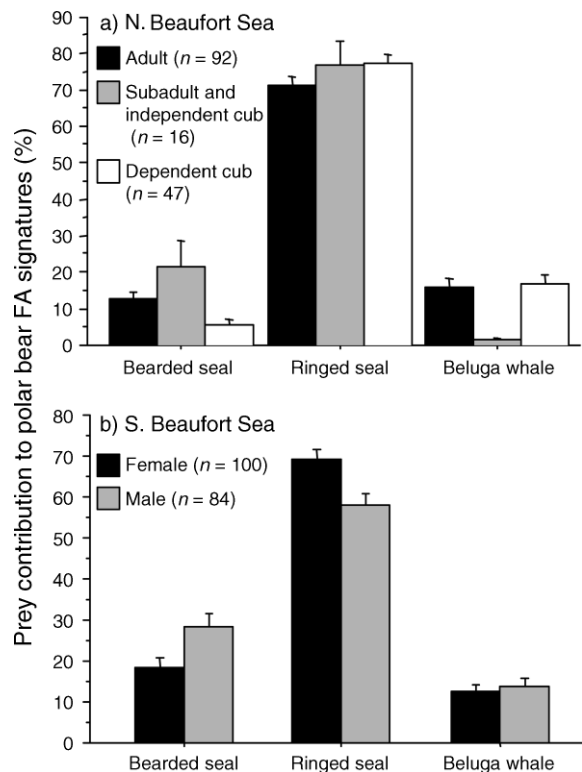


FIG. 7. Demographic differences in the diet composition of polar bears of all ages sampled between 1999 and 2004 in (a) Northern Beaufort Sea and (b) Southern Beaufort Sea; n = number of bears sampled. Polar bear diets differed by age in the northern region ($P = 0.007$), and by sex in the southern subpopulation ($P = 0.013$).

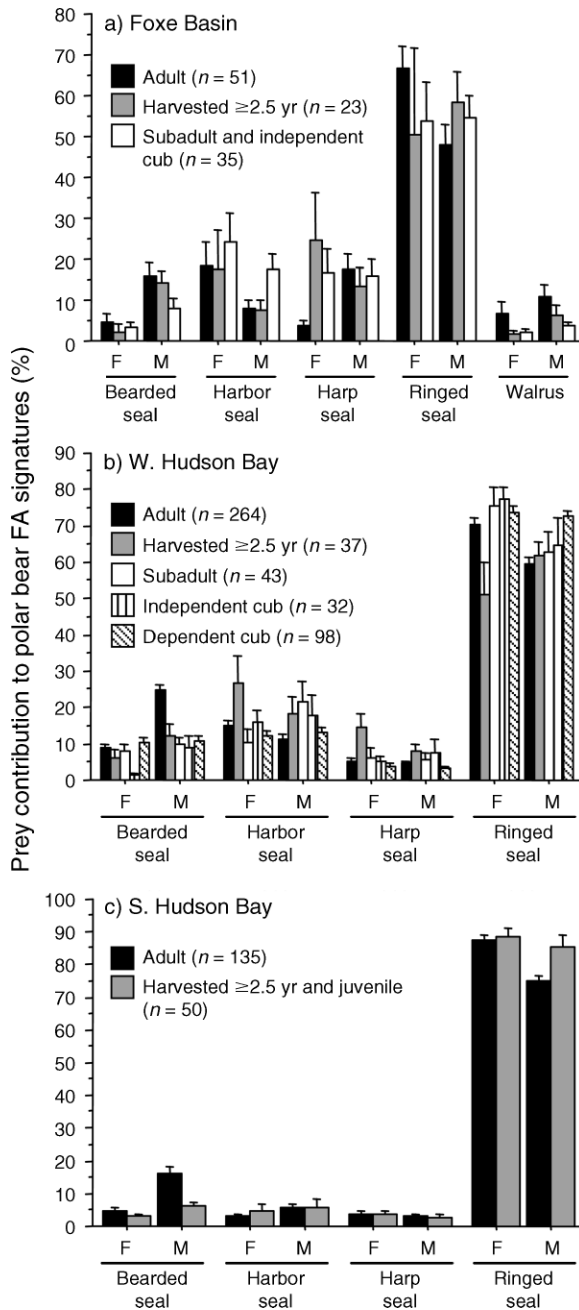


FIG. 8. Demographic differences in the diet composition of polar bears of all ages sampled between 1999 and 2004 in (a) FoXe Basin, (b) Western Hudson Bay, and (c) Southern Hudson Bay; n = number of bears sampled. Diets varied by sex and by age in all three subpopulations ($P < 0.030$) and were affected by sex \times age interactions in Southern ($P = 0.013$) and Western ($P < 0.001$) Hudson Bay. A nearly significant sex \times age interaction was found in FoXe Basin bears ($P = 0.056$).

among male bears than females. In Western Hudson Bay, adult ($H' = 0.744$) and harvested (≥ 2.5 yr old) ($H' = 0.778$) bears had the most diverse diets, whereas subadults ($H' = 0.637$) and independent cubs ($H' =$

0.630) had the least diverse diets. In Southern Hudson Bay, a significant age \times sex interactive effect ($P = 0.018$) was driven by relatively high diversity among adult males and low diversity among all other age and sex classes.

Seasonal differences in polar bear diets

The diets of independent-age bears differed between spring–summer and fall–winter in FoXe Basin ($P = 0.033$), Gulf of Boothia ($P = 0.001$), and Southern Hudson Bay ($P = 0.005$). No multivariate seasonal trends were apparent in Lancaster Sound ($P = 0.204$), Baffin Bay ($P = 0.386$), or Davis Strait ($P = 0.113$). However, in both Lancaster Sound and Baffin Bay, beluga whale tended to contribute more to polar bear diets in spring–summer than fall–winter (Fig. 10a, b). Despite the lack of a multivariate seasonal effect in Davis Strait, consumption of harp seal was higher in spring–summer than in fall–winter ($P = 0.015$; Fig. 10d), especially among female bears. Polar bears in the Gulf of Boothia consumed significantly more beluga whale in spring–summer ($P = 0.001$) and more ringed seal in fall–winter ($P < 0.001$; Fig. 10c), whereas bears in FoXe Basin consumed the most harbor seal in fall–winter ($P =$

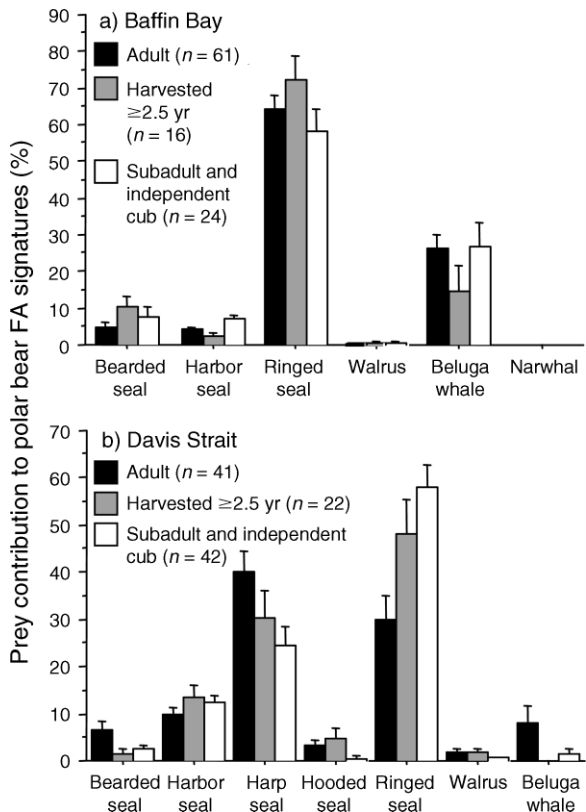


FIG. 9. Demographic differences in the diet composition of polar bears of all ages sampled between 1999 and 2004 in (a) Baffin Bay and (b) Davis Strait; n = number of bears sampled. Diets differed by age ($P < 0.040$) but not by sex ($P > 0.400$) in each region.

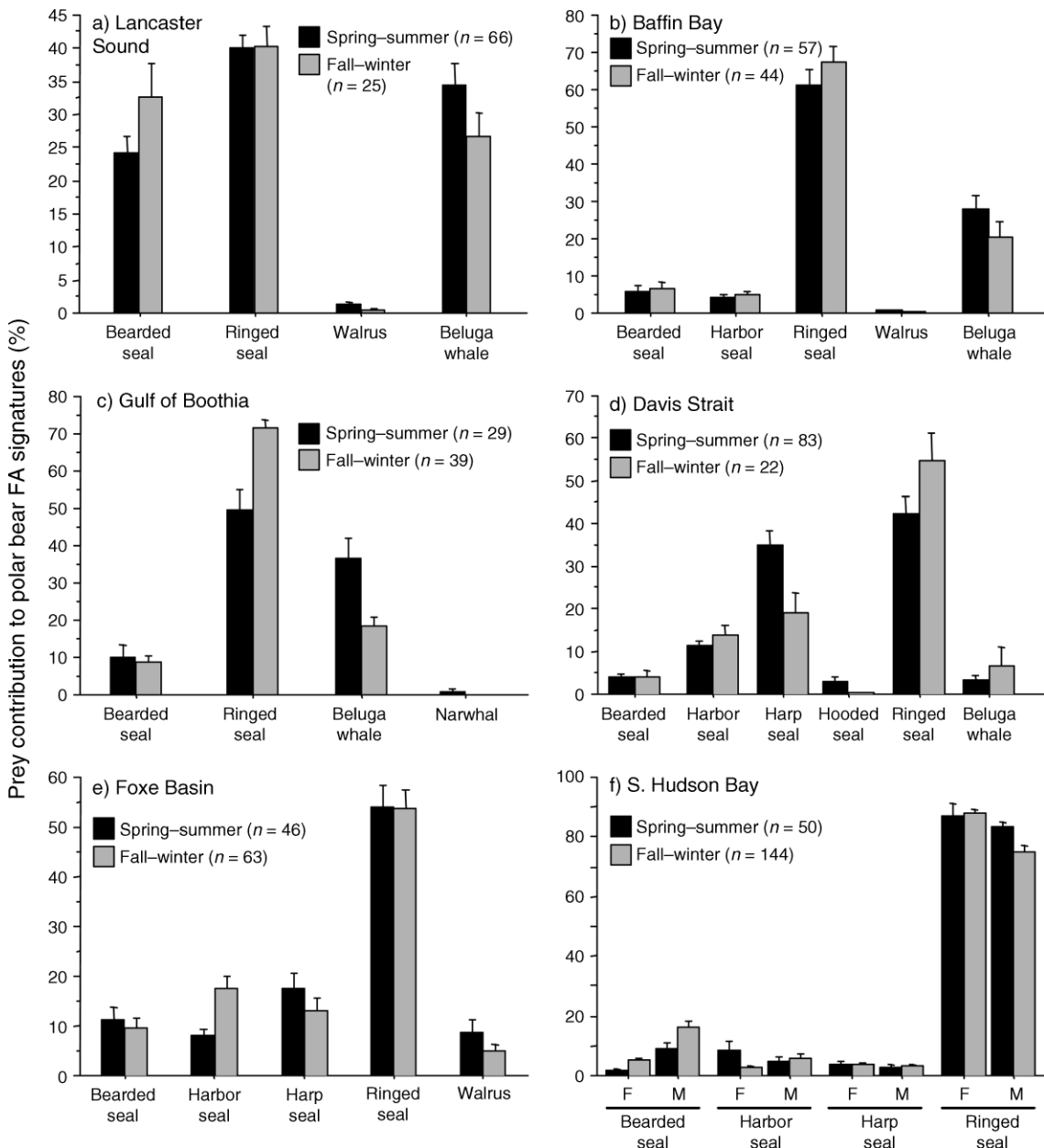


FIG. 10. Seasonal differences in the diet composition of independent-age polar bears (≥ 2.5 yr) in six Canadian subpopulations; n = number of samples (some bears were sampled in multiple time periods). Diets differed significantly by season in Gulf of Boothia ($P = 0.001$), Foxe Basin ($P = 0.033$), and S. Hudson Bay ($P = 0.005$). A univariate seasonal effect on harp seal consumption ($P = 0.015$) was found in Davis Strait.

0.004; Fig. 10e). In Southern Hudson Bay, seasonal ($P = 0.005$) and sex \times seasonal effects ($P = 0.031$) were driven by spring-to-fall increases in bearded seal consumption ($P = 0.001$) and decreases in ringed seal consumption ($P = 0.003$) in male bears (Fig. 10f). Females consumed more harbor seal in spring than in the fall ($P = 0.023$). The fall increase in bearded seal consumption among Southern Hudson Bay bears generated greater diet diversity in fall-winter ($H' = 0.490$) than spring-summer ($H' = 0.450$, $P = 0.038$).

Interannual differences in polar bear diets

Because polar bear tissue samples were collected sporadically and opportunistically over time in some regions (Appendix A), gaps were present in some data sets and samples often had to be grouped across several years. Nevertheless, longer-term temporal changes in polar bear diets were still apparent (Fig. 11). In the Northern Beaufort Sea, bearded seal consumption declined somewhat in 2000 ($P = 0.135$; Fig. 11a) before

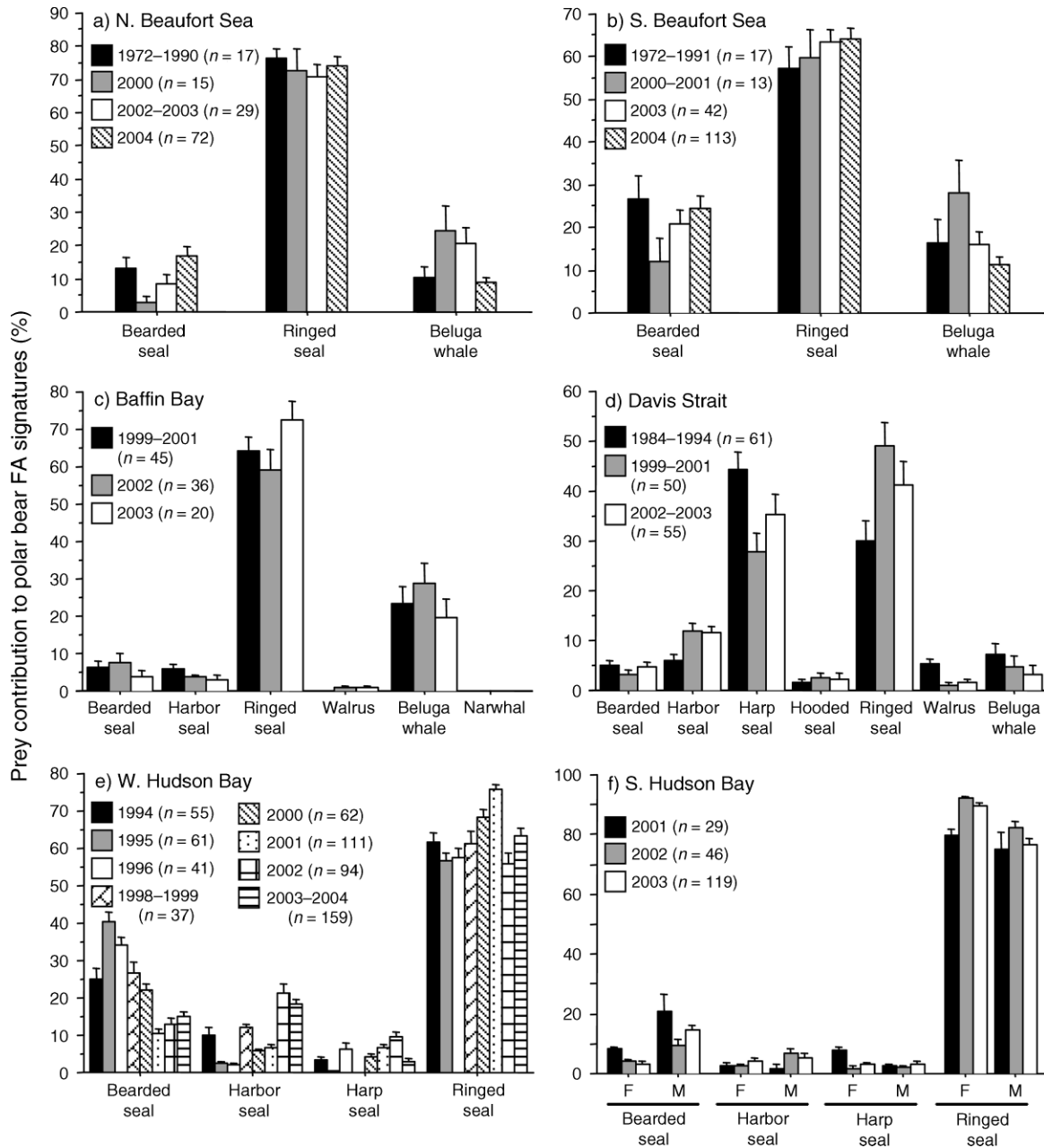


FIG. 11. Interannual differences in the diet composition of independent-age polar bears (≥ 2.5 yr) in six Canadian subpopulations; n = number of samples. Data from males (M) and females (F) are presented separately in regions with a year \times sex interaction (panel f, Southern Hudson Bay; $P = 0.022$). Diets differed across years in each region ($P < 0.020$) except Southern Beaufort Sea ($P = 0.094$). Note differing y-axis scales.

rebounding in 2004 ($P = 0.010$). An inverse trend occurred in beluga whale consumption, which more than doubled between 1972–1990 and 2000 ($P = 0.034$) before declining to earlier levels. Interannual differences in the Southern Beaufort Sea were not significant ($P = 0.094$) but the trends were similar to those of the Northern Beaufort Sea (Fig. 11b). A general shift toward more ringed seal and less beluga whale in the diets of Southern

Beaufort bears produced a significant decline in diet diversity ($P = 0.018$).

In Baffin Bay, interannual differences in polar bear diets ($P = 0.003$) were driven by a decline in harbor seal consumption between 1999–2001 and 2003 ($P = 0.048$) and a concomitant increase in walrus consumption ($P = 0.001$; Fig. 11c). In contrast, bears in Davis Strait increased harbor seal ($P = 0.002$) and decreased walrus ($P < 0.001$) consumption (Fig. 11d). The contribution of

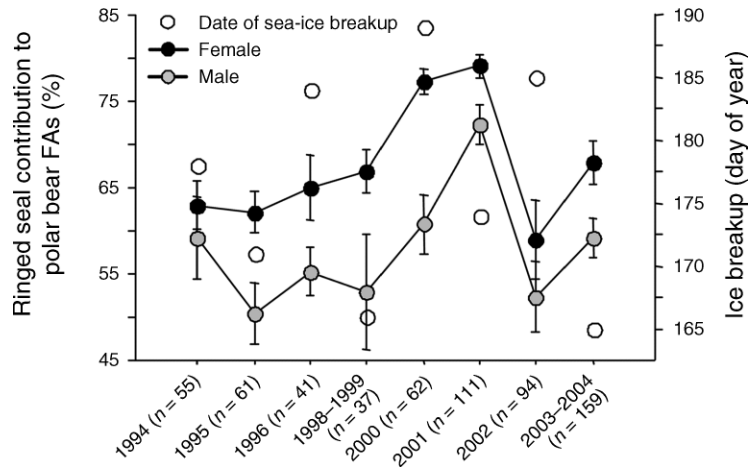


FIG. 12. Interannual variability in the contribution (mean \pm SE) of ringed seal to the FA signatures of independent-age polar bears (≥ 2.5 yr; $n = 620$ individuals), in relation to timing of sea-ice breakup (Day 1 = 1 January) in Western Hudson Bay (see Stirling et al. 1999). No significant relationship between date of sea-ice breakup and the consumption of ringed seal ($P = 0.903$) or any other prey species ($P > 0.090$) was present.

harp seal to Davis Strait diets declined from the 1984–1994 period to 1999–2001 ($P = 0.002$), while ringed seal increased over the same period ($P = 0.002$). In 2002–2003, the consumption of both species returned to levels that did not differ from 1984–1994 ($P > 0.060$).

In Western Hudson Bay, diets differed significantly over a 10-year period ($P < 0.001$; Fig. 11e). In general, the consumption of bearded seal declined while ringed seal first declined, then increased, and declined again. Between 1995 and 2001 the contribution of bearded seal to polar bear diets declined by 73% while the contribution from ringed seal increased by 33%. Harbor seal and harp seal were consumed in relatively minor amounts, although harbor seal consumption increased significantly between the mid-1990s and mid-2000s ($P < 0.001$). After a brief spike in 1996, harp seal consumption also increased steadily from 1998 to 2002 ($P < 0.001$) before declining again in 2003–2004 ($P < 0.001$).

Although the diets of bears in Southern Hudson Bay were dominated by ringed seals throughout the study, some interannual trends were apparent. Bearded seal consumption declined among both females ($P = 0.041$) and males ($P = 0.013$), although in the latter it increased again in 2003 ($P = 0.028$; Fig. 11f). Among female bears, harp seal consumption declined ($P < 0.001$) as ringed seal consumption increased ($P = 0.001$) between 2000 and 2003. The different interannual changes observed in male and female bears in Southern Hudson Bay resulted in a significant year \times sex interaction ($P = 0.022$). In contrast, in Western Hudson Bay, for which there was a far more comprehensive data set, interannual trends were consistent in both sexes (year \times sex interaction, $P = 0.162$). In this subpopulation, male bears always consumed more bearded seal and less ringed seal than did females.

Diet diversity also changed over time in the two Hudson Bay subpopulations ($P < 0.002$). In Southern Hudson Bay, diversity declined among independent-age

female bears between 2001 ($H' = 0.667$) and 2002 ($H' = 0.297$) and remained low in 2003 ($H' = 0.350$). Shannon-Wiener values remained relatively high among male bears across all three years (mean $H' = 0.561$). Sex-specific trends in diet diversity resulted in a significant year \times sex interaction ($P = 0.026$). In Western Hudson Bay, diet diversity was lowest in 2001 ($H' = 0.659$), when diets were dominated by ringed seals, and highest in 1996 ($H' = 0.799$), when diets contained relatively high levels of bearded and harp seal.

To investigate the potential effects of timing of sea-ice breakup on polar bear foraging habits in Western Hudson Bay, we compared the date of breakup (calculated as the date when surface waters were 50% ice covered; see Stirling et al. 1999) with QFASA diet estimates. Regression analyses indicated no significant relationship between breakup and the consumption of ringed seal ($P = 0.903$; Fig. 12) or any other prey species ($P > 0.090$).

DISCUSSION

As broadly distributed top predators, polar bears can provide important insights into the structure and functioning of arctic food webs. In addition to quantifying the trophic relationships between polar bears and marine mammals across the Canadian Arctic, this study identified some of the intrinsic and extrinsic factors that affect polar bear foraging. These results represent a significant step towards a thorough understanding of the arctic ecosystem and establish an important baseline for detecting future changes in arctic marine food webs.

Polar bear fatty acid signatures

As found in other studies of high latitude marine mammals (e.g., Iverson et al. 1997, Thiemann et al. 2007b, 2008), polar bear fatty acid (FA) signatures

differed spatially, temporally, and demographically. Spatially, the greatest similarities were observed between adjacent subpopulations, consistent with greater likelihood of shared prey resources. For instance, the strong similarities among bears in the Northern and Southern Beaufort Sea likely resulted from both subpopulations foraging around the Cape Bathurst polynya. This annually recurring area of open water in the winter sea ice extends across the border of the two subpopulations in Amundsen Gulf (Fig. 1; Stirling 1997) and is an area of high biological productivity and marine-mammal abundance (Stirling et al. 1981). Similarly, bears in Baffin Bay and Lancaster Sound may have been attracted to the large numbers of marine mammals associated with the high productivity of the North Water polynya in northern Baffin Bay (Stirling et al. 1981, Stirling 1997, Klein et al. 2002).

The polar bear subpopulations presented in Fig. 1 are based on extensive analyses of polar bear movement patterns (e.g., Stirling et al. 1977b, 1980, Bethke et al. 1996, Taylor et al. 2001, Amstrup et al. 2004) and genetic relationships (Paetkau et al. 1995, 1999). Mark-recapture and telemetry data demonstrate that polar bears restrict their movements and reproductive activities to within the subpopulation regions (e.g., Stirling et al. 1999, Amstrup et al. 2000, Taylor et al. 2001, Mauritzen et al. 2002). However, where physical barriers (such as extensive areas of land or multi-year ice) do not exist, individual bears may cross management boundaries (Schweinsburg and Lee 1982, Schweinsburg et al. 1982, Bethke et al. 1996). These occasional movements have resulted in smaller genetic differences between some adjacent subpopulations (Paetkau et al. 1999) and have likely contributed to the patterns of FA similarity observed in Fig. 2. In contrast, subpopulations that are separated from each other by geographical barriers or large distances were more distinct in their FA signatures (Fig. 2a). The Gulf of Boothia, Foxe Basin, and M'Clintock Channel subpopulations, although adjacent to each other, are separated by relatively broad land masses (Fig. 1) and all three groups were well separated in the cluster analysis (Fig. 2a). Conversely, the foraging ranges of bears in Western and Southern Hudson Bay overlap during winter (Stirling and Derocher 1993, Taylor and Lee 1995, Stirling et al. 1999) and bears in both areas have access to some of the same offshore prey populations.

Prey migration routes may also result in bears in different regions having access to the same prey populations. For instance, beluga whales commonly migrate between the Lancaster Sound and Baffin Bay regions (Richard et al. 1998, 2001, Heide-Jørgensen et al. 2003) or between Hudson Bay and Foxe Basin (Sergeant 1973). Harp seals follow the sea ice as it retreats in summer through Hudson Strait (Sergeant 1965), and such movements may have contributed to the FA similarities of bears in Foxe Basin, Hudson Bay, and Davis Strait (Fig. 2).

Regional differences in polar bear diets

Ringed seals were the dominant prey of polar bears in every region of the Canadian Arctic, whether expressed as a proportion of polar bear FA signatures (Fig. 4) or as the relative number of prey taken (Fig. 5). This trend reflects the close ecological and evolutionary relationships between polar bears and ringed seals (Stirling 1977, 1983, Hammill and Smith 1991, Kingsley and Stirling 1991, Stirling and Øritsland 1995) and the relatively ubiquitous distribution and high abundance of ringed seals throughout the Canadian Arctic (e.g., Kingsley et al. 1985, Smith et al. 1991). It is probably also significant that ringed seals are among the smallest of potential prey species and so should be most accessible to bears of all age and sex classes. Considering the close association between ringed seal abundance and their consumption by polar bears (Stirling and Øritsland 1995), the dietary contributions of other prey species may also reflect the regional abundance of those prey.

Stirling and Archibald (1977) observed that bearded seals were more important as prey to polar bears in the western Arctic than the eastern Arctic, a trend that is consistent with our overall regional data (Fig. 4). Because little is known about geographic differences in bearded seal availability, spatial patterns of bearded seal consumption are difficult to explain. For instance, the reasons behind the greater consumption of bearded seal in the Southern Beaufort Sea than the Northern Beaufort Sea (Fig. 6a) are not clear. However, a similar regional trend was observed by Thiemann et al. (2007a), who found higher levels of a specific bearded seal FA biomarker in Southern Beaufort Sea bears than in the northern subpopulation. Iverson et al. (2006) also found higher bearded seal consumption among polar bears sampled in the Southern Beaufort Sea between 1972 and 1991.

This study further quantifies the importance of harp seals in the diets of some polar bears (Fig. 4). From opportunistic observations, Derocher et al. (2002) estimated that harp seal biomass comprised 15% of the diets of polar bears in Svalbard and the Barents Sea in early summer. More recently, Iverson et al. (2006) used quantitative fatty acid signature analysis (QFASA) in a smaller study and found that harp seal accounted for 49% of the FA profiles of polar bears sampled in Davis Strait between 1984 and 1999. In the past few decades the northwest Atlantic harp seal population has exceeded 5 million individuals (DFO 2005) and this level of abundance appears to be reflected in their consumption by polar bears. Although the level of consumption reported here is less than that found by Iverson et al. (2006), this may be related to changes in numbers of harp seals or their accessibility to the bears (see *Interannual differences in polar bear diets*, below).

We were unable to estimate the importance of harp seal in the diets of bears in the High Arctic. When harp seals sampled in Davis Strait were used to model the diets of polar bears in the far North, the QFASA model

had difficulty distinguishing between harp seals and other prey—primarily ringed seals. The reason for this uncertainty was not clear as harp seals were accurately identified in diet simulations (Fig. 3) and appeared to be clearly resolved in the modeled diets of polar bears in Hudson Bay, Foxe Basin, and Davis Strait (Fig. 4). Considering that harp seals arrive in the High Arctic during the open water season and are likely relatively inaccessible to polar bears, and further considering the absence of recorded observations of polar bears hunting harp seals in the High Arctic, it seems unlikely that harp seal consumption would be particularly high in these areas. However, the possibly ambiguous modeling results from Lancaster Sound, Baffin Bay, and Gulf of Boothia point to the need for greater prey sampling in those areas, as well as a more thorough understanding of seal distribution in the High Arctic.

This study is the first to quantify the consumption of beluga whale by polar bears. Numerous observations of polar bears feeding on beluga carcasses have suggested that whales might be a significant food source for polar bears (Freeman 1973, Heyland and Hay 1976, Lowry et al. 1987, Smith and Sjare 1990, Rugh and Sheldon 1993), but such anecdotal reports do not provide information on how often this occurs or how important belugas are in the diet of bears. Belugas may become especially vulnerable to predation during their seasonal migrations when they become entrapped in small openings in the sea ice. Lowry et al. (1987) reported the killing of at least 40 beluga whales at a single ice entrapment in the Bering Sea. In some areas, bears may also scavenge on the remains of belugas killed by Inuit hunters or on the carcasses of whales that wash ashore. Given the very large size of beluga whales compared to other polar bear prey, relatively few individuals would need to be killed to account for the observed contributions to polar bear FA signatures (see Fig. 5). The possible effects of changing ice conditions on beluga whale distribution, ice entrapment, and vulnerability to predation are difficult to predict (Heide-Jørgensen and Laidre 2004) and warrant further study.

Regional trends in diet composition also revealed important trophic linkages between polar bears and other, more minor, prey species. For instance, harp seals may migrate in large numbers to the area of Foxe Basin near Southampton Island (Sergeant 1976). Consistent with this, harp seal was relatively common in the diets of bears in Foxe Basin and the northern region of Western Hudson Bay (Fig. 6c). The relatively high consumption of walrus by polar bears in Foxe Basin was also consistent with the regional abundance of this species (DFO 2002).

Our results quantitatively confirm that polar bears prey (or in some cases likely scavenge) on species beyond ringed seals and bearded seals. Previous anecdotal reports of predation on other marine mammals have provided an indication of the broader foraging patterns quantified in this study. Polar bears appear to be capable

of opportunistically altering their foraging tactics (Kok and Nel 2004) to take advantage of locally abundant food resources (e.g., harp seals in the whelping patch off Newfoundland) as well as effectively hunting large-bodied and energy-rich prey (e.g., walrus, beluga whales). These findings suggest that at least some polar bears may be able to cope with a fluctuating arctic environment by adapting their foraging habits to suit local conditions. However, on a larger scale, polar bear diets are dominated by ringed seals and alternative prey species are likely not abundant enough to affect this ecological dependency.

Demographic differences in polar bear diets

Consistent with our hypothesis, adult male polar bears were the primary consumers of bearded seal. Because of their large size (up to 350–500 kg), mature bearded seals may be too large to be routinely killed by juveniles or adult female bears, which are roughly half the size of adult males (Atkinson et al. 1996, Derocher et al. 2005). It is therefore likely that much of the bearded seal fat detected in adult female or younger bears results from scavenging kills made by adult males or possibly their own predation on younger (smaller) bearded seals.

The similarity of adults and dependent cubs in the consumption of bearded seal and beluga whale (Figs. 7a and 8b) suggests that dependent bears have access to larger prey items occasionally killed or scavenged by their mother. In several areas, polar bears (especially males) appeared to switch to larger prey by consuming relatively more bearded seal, hooded seal, or walrus with increasing age (Figs. 8 and 9b). Several factors likely contributed to such age- and sex-specific trends. For instance, larger male bears may require larger prey in order to meet higher absolute energy requirements (Clutton-Brock et al. 1987, Nagy 1987). Switching to larger prey species that are less accessible to smaller bears may also reduce intraspecific competition (Clarke et al. 1998, Kie and Bowyer 1999). Finally, differences in foraging patterns may arise from spatial segregation among demographic groups (Wielgus and Bunnell 1995, McLoughlin et al. 2002); females with dependent cubs apparently reduce the risk of infanticide by adult males by focusing their hunting effort on ringed seals on landfast ice. Adult males, meanwhile, forage more extensively offshore along the floe edge, where bearded seals are more abundant (Stirling et al. 1993). Clearly, the potential factors affecting demographic feeding patterns are not mutually exclusive and all may play a role in polar bear populations.

Intraspecific differences in dietary diversity have been observed in a variety of predators including marine mammals (Beck et al. 2007), mustelids (Birks and Dunstone 1985), and reptiles (Houston and Shine 1993). Differences in dietary-niche breadth may be a consequence of larger animals being either (1) less selective, perhaps in order to meet increased energy requirements (e.g., Clutton-Brock et al. 1987), or (2)

more selective, and able to focus predation on larger, higher-quality prey (Houston and Shine 1993). Among polar bears, large adult males had the greatest dietary-niche breadth likely because of their ability to capture large prey as well as take kills away from smaller bears. The broad dietary niche of harvested (≥ 2.5 yr old) bears may reflect the diverse mix of age classes within the harvested group (independent cubs, subadults, and adults). It may also indicate that large, younger bears have the physical ability to obtain large-bodied prey, but are less selective foragers than adults—a pattern of age-related diet diversity that has been observed in grey seals (Beck et al. 2007). Overall, the ability to diversify their diets may afford prime-age polar bears (5–19 years old) the greatest protection from large-scale environmental disturbance (Regehr et al. 2007).

Seasonal differences in polar bear diets

As expected, considering the dramatic seasonal variability of the Arctic, polar bear diets differed significantly through the year. The consumption of migratory species, which may be absent during winter months, tended to increase in spring and summer as the ice receded and was replaced by more productive open water. Bears in the Gulf of Boothia shifted their diets from ringed seals in fall–winter to beluga whale in spring–summer (Fig. 10c). These bears also showed a slight seasonal increase in their consumption of narwhal, which summer in this area (Laidre and Heide-Jørgensen 2005).

The spring migration of harp seals into Foxe Basin (Sergeant 1976) was reflected in the diets of bears (Fig. 10e). The trend toward increased harp seal consumption in Davis Strait in spring–summer was likely the result of increased harp seal availability and abundance during the spring breeding season off the coasts of Newfoundland and Labrador (Stirling and Parkinson 2006).

Interannual differences in polar bear diets

The lack of interannual differences in diets among polar bears in Lancaster Sound, Gulf of Boothia, and Foxe Basin were likely a consequence of limited temporal distribution of samples (Appendix A). In areas where diets did show year-to-year variability, polar bear foraging may have been affected by large-scale food web processes.

The similarity of interannual trends in the Northern and Southern Beaufort Sea (Fig. 11) suggests that these changes were related to larger ecological shifts, especially between 2000 and 2004. Although the exact causes of such large-scale changes are uncertain, the reproductive success of ringed seals and polar bears has fluctuated over extended periods. Ringed seal recruitment and abundance in the eastern Beaufort declined in the mid-1970s and again in the mid-1980s (Stirling et al. 1977a, 1982, Harwood and Stirling 1992). These periods of heavy ice and low seal abundance were associated with declines in polar bear reproduction (Stirling et al.

1977a, Stirling and Lunn 1997, Stirling 2002) and it is possible that polar bear diets may have also changed. However, our data indicate that ringed seal consumption in this area was consistent over the course of our study (Fig. 11). Although we did not have samples from bears during either of the periods of low ringed seal availability (Appendix A), these results, along with the documented declines in polar bear reproduction, suggest that ringed seal consumption by polar bears may be constrained and that polar bears in the Beaufort Sea have a limited ability to sufficiently compensate with alternative prey when ringed seals, especially young of the year, become scarce.

In Davis Strait the dominant interannual trend in polar bear diets was a decline in the contribution of harp seal between 1984–1994 and 1999–2001 (Fig. 11d). During this period, the primary prey of polar bears switched from harp seal to ringed seal. Using the same 1984–1994 samples, Iverson et al. (2006) found that harp seal accounted for 49% of polar bear diets in Davis Strait—very close to our estimate of 44%. Iverson et al. (2006) pointed out that the dominance of harp seal in polar bear diets was consistent with the well-documented growth of the northwest Atlantic harp seal population since the early 1970s (Hammill and Stenson 2005). However, our data indicate that harp seal consumption by polar bears has declined since the mid-1990s, a trend that may be related to two factors: (1) the reestablishment of the commercial harp seal harvest and, (2) climate-related changes in ice conditions.

Between 1983 and 1995 the northwest Atlantic harp seal harvest averaged 52 000 seals per year. Between 1996 and 2004 annual catches ranged from 92 000 to 366 000 and averaged 257 000 individuals (DFO 2005). Although this harvest appears to have held the overall population at a steady size since 1996 (Hammill and Stenson 2005), 95% of the catch has been young-of-the-year seals (DFO 2005), which may also be the primary target of polar bears. In addition, the area of Davis Strait southeast of Baffin Island has experienced some of the greatest warming of any part of the Canadian Arctic over the last two decades (Comiso and Parkinson 2004). Because harp seal pups, like pups of other ice-breeding phocids (Stirling 2005), are dependent on the sea-ice platform for several weeks after weaning, reductions in the area and extent of sea ice may affect the survival and abundance of harp seal pups (Johnston et al. 2005, DFO 2007). Temporal or spatial reductions in the amount of stable sea ice may also reduce the ability of polar bears to access harp seal whelping and molting patches. The possible impacts of climate change and harp seal harvest levels on the condition, reproduction, and abundance of polar bears in Davis Strait warrant further study.

Partly because of its southern geographic position and accessibility from the town of Churchill, the Western Hudson Bay subpopulation is the best-studied group of polar bears in the world (e.g., Stirling et al. 1999). Consequently, we were able to rigorously examine

interannual trends in the diets of these bears over a decade-long period. Although the population trends of other marine mammals in Hudson Bay are not as well understood, our data, combined with the limited information available on seal populations, indicate that the Hudson Bay ecosystem has experienced significant fluctuations over the past decade.

In late summer the sea ice of Hudson Bay melts completely and the entire polar bear subpopulation is forced to fast on land for approximately four months (Stirling et al. 1977b). Increasing air temperatures over Hudson Bay in spring (e.g., Skinner et al. 1998, Comiso 2006, Serreze and Francis 2006) appear to be driving a trend toward progressively earlier sea-ice breakup, albeit with substantial interannual variation. At present, the average date of breakup is about 3 weeks earlier than it was 30 years ago (Gough et al. 2004, Stirling et al. 2004, Stirling and Parkinson 2006). One consequence of this earlier breakup is that, on average, polar bears have less time each year to forage on the sea ice while at the same time being forced to fast on shore for progressively longer periods with less stored fat on their bodies. As a result, the body condition of adult polar bears, as well as their rates of reproduction and survival, have declined over time (Stirling et al. 1999, Derocher et al. 2004, Stirling and Parkinson 2006), leading to an overall population decline of about 22% since 1987 (Regehr et al. 2007). Although this trend appears to have been initiated by reduced recruitment arising from poorer body condition, the continuation of unsustainable polar bear harvest rates in Western Hudson Bay have also contributed to the decline in population size (Stirling and Parkinson 2006).

Polar bears prey heavily on newly weaned ringed seal pups. These young animals are inexperienced with predators and are 40–50% body fat by wet mass (Stirling and McEwan 1975, Stirling and Archibald 1977). Although the causative factors are uncertain, reproduction and recruitment of ringed seals in Western Hudson Bay were very low in 1991–1992 and 1998–1999 (Ferguson et al. 2005, Stirling 2005). However, consumption rates of ringed seal by polar bears were fairly steady throughout the study, and even increased slightly in 2000 and 2001. This increase may have been related to ringed seal reproductive rates, which appeared to increase sharply in 2000 (Stirling 2005). Also consistent with increased ringed seal availability in 2000, the average body mass of lone adult females (Stirling and Parkinson 2006) and the survival of all age classes of polar bears (Regehr et al. 2007) increased in 2000. In more recent years, diet, body mass, and survival returned to pre-2000 levels, but data on ringed seal recruitment were not available. Through the same period in Western Hudson Bay, bearded seal consumption declined sharply (Fig. 11e) although there are no other data on their abundance or reproductive success.

Iverson et al. (2006) reported an apparent correlation between date of sea-ice breakup and ringed seal

consumption, albeit on the basis of many fewer data points collected between 1994 and 1998. Such a trend was also apparent in our data, especially for male bears, between 1994 and 2000. The late breakup in 2000 may have contributed to the high ringed seal recruitment observed by Stirling (2005) and relatively high ringed seal consumption in 2001 (Fig. 12), but overall, there was no significant relationship between polar bear foraging and duration of sea ice. Clearly, the relationship between environment, ringed seal abundance, and polar bear foraging is more complex than a simple relationship with breakup date. The dietary shift away from bearded seal and towards species more common in open water (i.e., harp and harbor seals) is likely to be maintained if air temperatures and areas of open water continue to increase. However, the relatively steady contribution of ringed seal to polar bear diets, in spite of year-to-year changes in sea-ice duration and reproductive rates, suggest that no other species is sufficiently abundant and accessible enough to replace ringed seals in the diets of polar bears. If ringed seal abundance and reproductive success are declining in Western Hudson Bay, for whatever reason, it is likely to be part of the explanation for recent declines in the natality, condition, and abundance of the polar bears there.

In summary, this study represents a large-scale, ecosystem-based approach to studying arctic marine food webs using a top predator. By quantifying trophic interactions between polar bears and their prey, the results of the QFASA model provide important information on the structure and functioning of arctic food webs. Our data confirm in quantitative terms that polar bears forage beyond ringed and bearded seals. Polar bears of different age and sex classes may also specialize on different prey species. In areas where prey diversity is relatively rich, some bears appear to feed opportunistically on locally abundant species other than ringed and bearded seals. In regions where prey species are less diverse, the greater dependence of polar bears on ringed and bearded seals likely make them more sensitive to environmental change. The ability of QFASA to quantify dietary changes through time and between different geographic areas, suggests that its continued use and further development may facilitate identification of ecological shifts that might not otherwise be detectable, especially in the early stages.

ACKNOWLEDGMENTS

We are particularly grateful to the native hunters of Nunavut and Newfoundland and Labrador for collecting fat samples from marine mammals harvested in their subsistence hunts. J. M. Bourgeois, J. Beauchesne, and F. Piugattuk (Nunavut Wildlife Service), M. Campbell (Nunavut Department of Sustainable Development), and J. Rowell (Labrador Inuit Association) coordinated the submission of samples by hunters. Thanks to D. Andriashek, A. E. Derocher, N. J. Lunn, and E. Richardson for assistance with the collection of samples during mark–recapture studies. We also thank W. Bernhardt, B. Dunn, G. Gilchrist, L. Harwood, V. Lesage, D. Muir, M. Obbard, J. Palm, B. Sjare, C. Sonne-Hansen, G. Stenson, M. Taylor, and

S. Tucker for collecting and sharing samples. W. Blanchard helped to model polar bear diets, and K. Rouvinen-Watt ran the captive mink feeding experiments. N. J. Lunn and J. Iacozza provided data on breakup dates in Western Hudson Bay. We are grateful to J. Blair, D. Bowen, M. Leonard, and two anonymous reviewers for helpful comments on earlier versions of the manuscript and to S. Lang for her invaluable assistance in the laboratory. This study was primarily supported by Natural Sciences and Engineering Research Council (NSERC, Canada) and Killam Trust Scholarships to G. W. Thiemann, by NSERC operating and equipment grants to S. J. Iverson, the Polar Continental Shelf Project, and by the Canadian Wildlife Service. We are grateful to the following organizations for additional financial support: the Northern Scientific Training Program, Dr. Patrick Lett Student Bursary Fund, Government of Nunavut, Nunavut Wildlife Management Board, World Wildlife Fund (Canada and International), Fisheries and Oceans Canada, and the Churchill Northern Studies Centre.

LITERATURE CITED

- Ackman, R. G., and C. A. Eaton. 1966. Lipids of the fin whale (*Balaenoptera physalus*) from North Atlantic waters. III. Occurrence of eicosenoic and docosenoic fatty acids in the zooplankton *Meganyctiphanes norvegica* (M. Sars) and their effect on whale oil composition. *Canadian Journal of Biochemistry* 44:1561–1566.
- Amstrup, S. C., G. M. Durner, I. Stirling, N. J. Lunn, and F. Messier. 2000. Movements and distribution of polar bears in the Beaufort Sea. *Canadian Journal of Zoology* 78:948–966.
- Amstrup, S. C., T. L. McDonald, and G. M. Durner. 2004. Using satellite radiotelemetry data to delineate and manage wildlife populations. *Wildlife Society Bulletin* 32:661–679.
- Amstrup, S. C., I. Stirling, T. S. Smith, C. Perham, and G. W. Thiemann. 2006. Recent observations of intraspecific predation and cannibalism among polar bears in the southern Beaufort Sea. *Polar Biology* 29:997–1002.
- Anderson, M. J. 2001. Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences* 58:626–639.
- Atkinson, S. N., I. Stirling, and M. A. Ramsay. 1996. Growth in early life and relative body size among adult polar bears (*Ursus maritimus*). *Journal of Zoology* 239:225–234.
- Beck, C. A., S. J. Iverson, W. D. Bowen, and W. Blanchard. 2007. Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. *Journal of Animal Ecology* 76:490–502.
- Bentzen, T. W., E. H. Follmann, S. C. Amstrup, G. S. York, M. J. Wooller, and T. M. O'Hara. 2007. Variation in winter diet of southern Beaufort Sea polar bears inferred from stable isotope analysis. *Canadian Journal of Zoology* 85:596–608.
- Bethke, R., M. Taylor, S. C. Amstrup, and F. Messier. 1996. Population delineation of polar bears using satellite collar data. *Ecological Applications* 6:311–317.
- Birks, J. D. S., and N. Dunstone. 1985. Sex-related differences in the diet of the mink *Mustela vison*. *Holarctic Ecology* 8: 245–252.
- Bowen, W. D. 1997. Role of marine mammals in aquatic ecosystems. *Marine Ecology Progress Series* 158:267–274.
- Bradshaw, C. J. A., M. A. Hindell, N. J. Best, K. L. Phillips, G. Wilson, and P. D. Nichols. 2003. You are what you eat: describing the foraging ecology of southern elephant seals (*Mirounga leonina*) using blubber fatty acids. *Proceedings of the Royal Society of London, B* 270:1283–1292.
- Brockerhoff, H., R. J. Hoyle, and P. C. Hwang. 1967. Incorporation of fatty acids of marine origin into triglycerides and phospholipids of mammals. *Biochimica et Biophysica Acta* 144:541–548.
- Budge, S. M., S. J. Iverson, W. D. Bowen, and R. G. Ackman. 2002. Among- and within-species variability in fatty acid signatures of marine fish and invertebrates on the Scotian Shelf, Georges Bank, and southern Gulf of St. Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences* 59:886–898.
- Budge, S. M., S. J. Iverson, and H. N. Koopman. 2006. Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. *Marine Mammal Science* 22:759–801.
- Callaghan, T. V., and S. Jonasson. 1995. Arctic terrestrial ecosystems and environmental change. *Philosophical Transactions of the Royal Society of London, A* 352:259–274.
- Calvert, W., and M. A. Ramsay. 1998. Evaluation of age determination of polar bears by counts of cementum growth layer groups. *Ursus* 10:449–453.
- Calvert, W., and I. Stirling. 1990. Interactions between polar bears and overwintering walruses in the central Canadian High Arctic. *International Conference on Bear Research and Management* 8:351–356.
- Clarke, J., B. Manly, K. Kerry, H. Gardner, E. Franchi, S. Corsolini, and S. Focardi. 1998. Sex differences in Adélie penguin foraging strategies. *Polar Biology* 20:248–258.
- Clutton-Brock, T. H., G. R. Iason, and F. E. Guinness. 1987. Sexual segregation and density-related changes in habitat use in male and female red deer (*Cervus elaphus*). *Journal of Zoology, London* 211:275–289.
- Comiso, J. C. 2002. A rapidly declining perennial sea ice cover in the Arctic. *Geophysical Research Letters* 29:17-1–17-4.
- Comiso, J. C. 2006. Arctic warming signals from satellite observations. *Weather* 61:70–76.
- Comiso, J. C., and C. L. Parkinson. 2004. Satellite-observed changes in the Arctic. *Physics Today* 57:38–44.
- Dalsgaard, J., and M. St. John. 2004. Fatty acid biomarkers: validation of food web and trophic markers using ¹³C-labelled fatty acids in juvenile sandeel (*Ammodytes tobianus*). *Canadian Journal of Fisheries and Aquatic Sciences* 61:1671–1680.
- Derocher, A. E., M. Andersen, and Ø. Wiig. 2005. Sexual dimorphism of polar bears. *Journal of Mammalogy* 86:865–901.
- Derocher, A. E., N. J. Lunn, and I. Stirling. 2004. Polar bears in a warming climate. *Integrative and Comparative Biology* 44: 163–176.
- Derocher, A. E., and Ø. Wiig. 2002. Postnatal growth in body length and mass of polar bears (*Ursus maritimus*) at Svalbard. *Journal of Zoology, London* 256:343–349.
- Derocher, A. E., Ø. Wiig, and M. Andersen. 2002. Diet composition of polar bears in Svalbard and the western Barents Sea. *Polar Biology* 25:448–452.
- Derocher, A. E., Ø. Wiig, and G. Bangjord. 2000. Predation of Svalbard reindeer by polar bears. *Polar Biology* 23:675–678.
- DFO [Department of Fisheries and Oceans]. 2002. Atlantic walrus. DFO Stock Status Report E5-17, 18, 19, 20. Fisheries and Oceans Canada, Ottawa, Ontario, Canada.
- DFO [Department of Fisheries and Oceans]. 2005. Stock Assessment of northwest Atlantic harp seals (*Pagophilus groenlandicus*). *Canadian Science Advisory Secretariat Science Advisory Report* 2005/037. Fisheries and Oceans Canada, Ottawa, Ontario, Canada.
- DFO [Department of Fisheries and Oceans]. 2007. A review of ice conditions and potential impact on harp seal neonatal mortality in March 2007. *Canadian Science Advisory Secretariat Science Response* 2007/008. Fisheries and Oceans Canada, Ottawa, Ontario, Canada.
- Efron, B., and R. J. Tibshirani. 1998. *An introduction to the bootstrap*. Chapman and Hall, New York, New York, USA.
- Estes, J. A. 1995. Top level carnivores and ecosystem effects: questions and approaches. Pages 151–158 in C. G. Jones and J. H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, Toronto, Ontario, Canada.
- Ferguson, S. H., I. Stirling, and P. McLoughlin. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. *Marine Mammal Science* 21:121–135.

- Freeman, M. M. R. 1973. Polar bear predation on beluga in the Canadian Arctic. *Arctic* 26:162–163.
- Gagnon, A. S., and W. A. Gough. 2005. Trends in the dates of ice freeze-up and breakup over Hudson Bay, Canada. *Arctic* 58:370–382.
- Gaston, A. J., K. Woo, and J. M. Hipfner. 2003. Trends in forage fish populations in northern Hudson Bay since 1981, as determined from the diet of nestling thick-billed Murres, *Uria lomvia*. *Arctic* 56:227–233.
- Good, P. 2000. Permutation tests: a practical guide to resampling methods for testing hypotheses. Second edition. Springer-Verlag, New York, New York, USA.
- Gough, W. A., A. R. Cornwell, and L. J. S. Tsuji. 2004. Trends in seasonal sea ice duration in southwestern Hudson Bay. *Arctic* 57:299–305.
- Hammill, M. O., and T. G. Smith. 1991. The role of predation in the ecology of the ringed seal in Barrow Strait, Northwest Territories, Canada. *Marine Mammal Science* 7:123–135.
- Hammill, M. O., and G. B. Stenson. 2005. Abundance of northwest Atlantic harp seals (1960–2005). Canadian Science Advisory Secretariat. Research Document 2005/090. Fisheries and Oceans Canada, Ottawa, Ontario, Canada.
- Harwood, L. A., and I. Stirling. 1992. Distribution of ringed seals in the southeastern Beaufort Sea during late summer. *Canadian Journal of Zoology* 70:891–900.
- Heide-Jørgensen, M. P., and K. L. Laidre. 2004. Declining extent of open-water refugia for top predators in Baffin Bay and adjacent waters. *Ambio* 33:487–494.
- Heide-Jørgensen, M. P., P. Richard, R. Dietz, K. L. Laidre, J. Orr, and H. C. Schmidt. 2003. An estimate of the fraction of belugas (*Delphinapterus leucas*) in the Canadian High Arctic that winter in West Greenland. *Polar Biology* 26:318–326.
- Heyland, J. D., and K. Hay. 1976. An attack by a polar bear on a juvenile beluga. *Arctic* 29:56–57.
- Hobson, K. A., and I. Stirling. 1997. Low variation in blood $\delta^{13}\text{C}$ among Hudson Bay polar bears: implications for metabolism and tracing terrestrial foraging. *Marine Mammal Science* 13:359–367.
- Hobson, K. A., and H. E. Welch. 1992. Determination of trophic relationships within a High Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Marine Ecology Progress Series* 84:9–18.
- Houston, D., and R. Shine. 1993. Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake. *Journal of Animal Ecology* 62:737–748.
- Iverson, S. J., C. Field, W. D. Bowen, and W. Blanchard. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. *Ecological Monographs* 74:211–235.
- Iverson, S. J., K. J. Frost, and S. L. C. Lang. 2002. Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: factors contributing to among and within species variability. *Marine Ecology Progress Series* 241:161–181.
- Iverson, S. J., K. J. Frost, and L. F. Lowry. 1997. Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. *Marine Ecology Progress Series* 151:255–271.
- Iverson, S. J., S. L. C. Lang, and M. H. Cooper. 2001. Comparison of the Bligh and Dyer and Folch methods for total lipid determination in a broad range of marine tissue. *Lipids* 36:1283–1287.
- Iverson, S. J., O. T. Oftedal, W. D. Bowen, D. J. Boness, and J. Sampugna. 1995. Prenatal and postnatal transfer of fatty acids from mother to pup in the hooded seal. *Journal of Comparative Physiology, B* 165:1–12.
- Iverson, S. J., A. M. Springer, and A. S. Kitaysky. 2007. Seabirds as indicators of food web structure and ecosystem variability: qualitative and quantitative diet analyses using fatty acids. *Marine Ecology Progress Series* 352:235–244.
- Iverson, S. J., I. Stirling, and S. L. C. Lang. 2006. Spatial and temporal variation in the diets of polar bears across the Canadian Arctic: indicators of changes in prey populations and environment. Pages 98–117 in I. L. Boyd, S. Wanless, and C. J. Camphuysen, editors. *Top predators in marine ecosystems*. Cambridge University Press, New York, New York, USA.
- Johnston, D. W., A. S. Friedlaender, L. G. Torres, and D. M. Lavigne. 2005. Variation in sea ice cover on the east coast of Canada from 1969 to 2002: climate variability and implications for harp and hooded seals. *Climate Research* 29:209–222.
- Katona, S., and H. Whitehead. 1988. Are cetacea ecologically important? *Oceanography and Marine Biology Annual Review* 26:553–568.
- Kie, J. G., and R. T. Bowyer. 1999. Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. *Journal of Mammalogy* 80:1004–1020.
- Kingsley, M. C. S., and I. Stirling. 1991. Haul-out behaviour of ringed and bearded seals in relation to defence against surface predators. *Canadian Journal of Zoology* 69:1857–1861.
- Kingsley, M. C. S., I. Stirling, and W. Calvert. 1985. The distribution and abundance of seals in the Canadian High Arctic, 1980–82. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1189–1210.
- Kirsch, P. E., S. J. Iverson, and W. D. Bowen. 2000. Effect of a low-fat diet on body composition and blubber fatty acids of captive juvenile harp seals (*Phoca groenlandica*). *Physiological and Biochemical Zoology* 73:45–59.
- Klein, B., et al. 2002. Phytoplankton biomass, production and potential export in the North Water. *Deep Sea Research Part II: Topical Studies in Oceanography* 49:4983–5002.
- Kok, O. B., and J. A. J. Nel. 2004. Convergence and divergence in prey of sympatric canids and felids: opportunism or phylogenetic constraint? *Biological Journal of the Linnean Society* 83:527–538.
- Krebs, C. J. 1999. *Ecological methodology*. Second edition. Benjamin/Cummings, New York, New York, USA.
- Laidre, K. L., and M. P. Heide-Jørgensen. 2005. Winter feeding intensity of narwhals (*Monodon monoceros*). *Marine Mammal Science* 21:45–57.
- Legendre, P., and L. Legendre. 1998. *Numerical ecology*. Second edition. Elsevier Scientific Publishers, New York, New York, USA.
- Lowry, L. F., J. J. Burns, and R. R. Nelson. 1987. Polar bear, *Ursus maritimus*, predation on belugas, *Delphinapterus leucas*, in the Bering and Chukchi Seas. *Canadian Field-Naturalist* 101:141–146.
- Lunn, N. J., et al. 2002. Polar bear management in Canada 1997–2000. Pages 41–52 in N. J. Lunn, S. Schliebe, and E. W. Born, editors. *Polar bears: Proceedings of the 13th working meeting of the IUCN/SSC Polar Bear Specialist Group*, Nuuk, Greenland. IUCN, Gland, Switzerland.
- Mauritzen, M., A. E. Derocher, Ø. Wiig, S. E. Belikov, A. N. Boltunov, E. Hansen, and G. W. Garner. 2002. Using satellite telemetry to define spatial population structure in polar bears in the Norwegian and western Russian Arctic. *Journal of Applied Ecology* 39:79–90.
- McLoughlin, P. D., R. L. Case, R. J. Gau, D. H. Cluff, R. Mulders, and F. Messier. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. *Oecologia* 132:102–108.
- Nagy, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs* 57:111–128.
- Paetkau, D., S. C. Amstrup, E. W. Born, W. Calvert, A. E. Derocher, G. W. Garner, F. Messier, I. Stirling, M. K. Taylor, Ø. Wiig, and C. Strobeck. 1999. Genetic structure of the world's polar bear populations. *Molecular Ecology* 8:1571–1584.

- Paetkau, D., W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* 4:347–354.
- Parkinson, C. L. 2000. Variability of Arctic Sea ice: the view from space, an 18-year record. *Arctic* 53:341–358.
- Ramsay, M. A., and K. A. Hobson. 1991. Polar bears make little use of terrestrial food webs: evidence from stable-carbon isotope analysis. *Oecologia* 86:598–600.
- Ramsay, M. A., C. A. Mattacks, and C. M. Pond. 1992. Seasonal and sex differences in the structure and chemical composition of adipose tissue in wild polar bears (*Ursus maritimus*). *Journal of Zoology*, London 228:533–544.
- Regehr, E. V., N. J. Lunn, S. C. Amstrup, and I. Stirling. 2007. Effects of earlier sea ice breakup on survival and population size of polar bears in western Hudson Bay. *Journal of Wildlife Management* 71:2673–2683.
- Richard, P. R., M. P. Heide-Jørgensen, J. R. Orr, R. Dietz, and T. G. Smith. 2001. Summer and autumn movements and habitat use by belugas in the Canadian High Arctic and adjacent areas. *Arctic* 54:207–222.
- Richard, P. R., M. P. Heide-Jørgensen, and D. St. Aubin. 1998. Fall movements of belugas (*Delphinapterus leucas*) with satellite-linked transmitters in Lancaster Sound, Jones Sound, and northern Baffin Bay. *Arctic* 51:5–16.
- Rugh, D. J., and K. E. W. Shelden. 1993. Polar bears, *Ursus maritimus*, feeding on beluga whales, *Delphinapterus leucas*. *Canadian Field-Naturalist* 107:235–237.
- Sargent, J. R., R. J. Parkes, I. Mueller-Harvey, and R. J. Henderson. 1987. Lipid biomarkers in marine ecology. Pages 119–138 in M. A. Sleight, editor. *Microbes in the Sea*. Ellis Horwood, Chichester, UK.
- Schweinsburg, R. E., and L. J. Lee. 1982. Movement of four satellite-monitored polar bears in Lancaster Sound, Northwest Territories. *Arctic* 35:504–511.
- Schweinsburg, R. E., L. J. Lee, and P. B. Latour. 1982. Distribution, movement, and abundance of polar bears in Lancaster Sound, Northwest Territories. *Arctic* 35:159–169.
- Sergeant, D. E. 1965. Migrations of harp seal *Pagophilus groenlandicus* (Erxleben) in the northwest Atlantic. *Journal of the Fisheries Research Board of Canada* 22:433–464.
- Sergeant, D. E. 1973. Biology of white whales (*Delphinapterus leucas*) in western Hudson Bay. *Journal of the Fisheries Research Board of Canada* 30:1065–1090.
- Sergeant, D. E. 1976. History and present status of populations of harp and hooded seals. *Biological Conservation* 10:95–118.
- Serreze, M. C., and J. A. Francis. 2006. The Arctic on the fast track of change. *Weather* 61:65–69.
- Skinner, W. R., R. L. Jefferies, T. J. Carleton, R. F. Rockwell, and K. F. Abraham. 1998. Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. *Global Change Biology* 4:3–16.
- Smith, T. G. 1980. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. *Canadian Journal of Zoology* 58:2201–2209.
- Smith, T. G., M. O. Hammill, and G. Taugbøl. 1991. A review of the developmental, behavioural and physiological adaptations of the ringed seal, *Phoca hispida*, to life in the Arctic winter. *Arctic* 44:124–131.
- Smith, T. G., and B. Sjøre. 1990. Predation of belugas and narwhals by polar bears in nearshore areas of the Canadian High Arctic. *Arctic* 43:99–102.
- SPSS. 2000. SPSS for Windows, version 10.1 [computer program]. SPSS, Chicago, Illinois, USA.
- Stevens, J. 1986. Applied multivariate statistics for the social sciences. Lawrence Erlbaum Associates, Mahwah, New Jersey, USA.
- Stirling, I. 1974. Midsummer observations on the behavior of wild polar bears (*Ursus maritimus*). *Canadian Journal of Zoology* 52:1191–1198.
- Stirling, I. 1977. Adaptations of Weddell and ringed seals to exploit the polar fast ice habitat in the absence or presence of surface predators. Pages 741–748 in G. A. Llano, editor. *Proceedings of the third symposium on Antarctic biology*. Gulf Publishing Company, Houston, Texas, USA.
- Stirling, I. 1983. The evolution of mating systems in pinnipeds. Pages 489–527 in J. F. Eisenberg and D. G. Kleiman, editors. *Advances in the study of mammalian behavior*. Special Publication of the American Society of Mammalogists. University of Chicago Press, Chicago, Illinois, USA.
- Stirling, I. 1997. The importance of polynyas, ice edges, and leads to marine mammals and birds. *Journal of Marine Systems* 10:9–21.
- Stirling, I. 2002. Polar bears and seals in the eastern Beaufort Sea and Amundsen Gulf: a synthesis of population trends and ecological relationships over three decades. *Arctic* 55(Supplement) 1:59–76.
- Stirling, I. 2005. Reproductive rates of ringed seals and survival of pups in Northwestern Hudson Bay, Canada, 1991–2000. *Polar Biology* 28:381–387.
- Stirling, I., D. Andriashek, and W. Calvert. 1993. Habitat preferences of polar bears in the western Canadian Arctic in late winter and spring. *Polar Record* 29:13–24.
- Stirling, I., and W. R. Archibald. 1977. Aspects of predation of seals by polar bears. *Journal of the Fisheries Research Board of Canada* 34:1126–1129.
- Stirling, I., W. R. Archibald, and D. DeMaster. 1977a. Distribution and abundance of seals in the eastern Beaufort Sea. *Journal of the Fisheries Research Board of Canada* 34:976–988.
- Stirling, I., W. Calvert, and D. Andriashek. 1980. Population ecology studies of the polar bear in the area of southeastern Baffin Island. *Canadian Wildlife Service Occasional Paper Number 44*. Canadian Wildlife Service, Ottawa, Ontario Canada.
- Stirling, I., H. Cleator, and T. G. Smith. 1981. Marine mammals. Pages 45–58 in I. Stirling and H. Cleator, editors. *Polynyas in the Canadian Arctic*. Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Stirling, I., and A. E. Derocher. 1993. Possible impacts of climate warming on polar bears. *Arctic* 46:240–245.
- Stirling, I., C. Jonkel, P. Smith, R. Robertson, and D. Cross. 1977b. The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay. *Occasional Paper Number 33*. Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Stirling, I., M. Kingsley, and W. Calvert. 1982. The distribution and abundance of seals in the eastern Beaufort Sea, 1974–79. *Occasional Paper Number 47*. Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Stirling, I., and P. B. Latour. 1978. Comparative hunting abilities of polar bear cubs of different ages. *Canadian Journal of Zoology* 56:1768–1772.
- Stirling, I., and N. J. Lunn. 1997. Environmental fluctuations in arctic marine ecosystems as reflected by variability in reproduction of polar bears and ringed seals. Pages 167–181 in S. J. Woodin and M. Marquiss, editors. *Ecology of arctic environments*. Blackwell Science, Oxford, UK.
- Stirling, I., N. J. Lunn, and J. Iacozza. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic* 52:294–306.
- Stirling, I., N. J. Lunn, J. Iacozza, C. Elliott, and M. Obbard. 2004. Polar bear distribution and abundance on the southwestern Hudson Bay coast during open water season, in relation to population trends and annual ice patterns. *Arctic* 57:15–26.
- Stirling, I., and E. H. McEwan. 1975. The caloric value of whole ringed seals (*Phoca hispida*) in relation to polar bear (*Ursus maritimus*) ecology and hunting behavior. *Canadian Journal of Zoology* 53:1021–1027.
- Stirling, I., and N. A. Øritsland. 1995. Relationships between estimates of ringed seal (*Phoca hispida*) and polar bear (*Ursus maritimus*) populations in the Canadian Arctic. *Canadian Journal of Fisheries and Aquatic Sciences* 52:2594–2612.

- Stirling, I., and C. L. Parkinson. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic* 59:261–275.
- Stirling, I., E. Richardson, G. W. Thiemann, and A. E. Derocher. 2008. Unusual predation attempts of polar bears on ringed seals in the southern Beaufort Sea: possible significance of changing spring ice conditions. *Arctic* 61:14–22.
- Stirling, I., C. Spencer, and D. Andriashek. 1989. Immobilization of polar bears (*Ursus maritimus*) with Telazol in the Canadian Arctic. *Journal of Wildlife Diseases* 25:159–168.
- Stone, I. R., and A. E. Derocher. 2007. An incident of polar bear infanticide and cannibalism on Phippsøya, Svalbard. *Polar Record* 43:171–173.
- Taylor, M. K., S. Akeagok, D. Andriashek, W. Barbour, E. W. Born, W. Calvert, H. D. Cluff, S. Ferguson, J. Laake, A. Rosing-Asvid, I. Stirling, and F. Messier. 2001. Delineating Canadian and Greenland polar bear (*Ursus maritimus*) populations by cluster analysis of movements. *Canadian Journal of Zoology* 79:690–709.
- Taylor, M. K., T. Larsen, and R. E. Schweinsburg. 1985. Observations of intraspecific aggression and cannibalism in polar bears (*Ursus maritimus*). *Arctic* 38:303–309.
- Taylor, M. K., and J. Lee. 1995. Distribution and abundance of Canadian polar bear populations: a management perspective. *Arctic* 48:147–154.
- Thiemann, G. W. 2006. Continental scale variation in polar bear (*Ursus maritimus*) diets and the fatty acid signatures of their marine mammal prey. Dissertation. Dalhousie University, Halifax, Nova Scotia, Canada.
- Thiemann, G. W., S. M. Budge, and S. J. Iverson. 2004. Determining blubber fatty acid composition: a comparison of *in situ* direct and traditional methods. *Marine Mammal Science* 20:284–295.
- Thiemann, G. W., S. M. Budge, S. J. Iverson, and I. Stirling. 2007a. Unusual fatty acid biomarkers reveal age- and sex-specific foraging in polar bears (*Ursus maritimus*). *Canadian Journal of Zoology* 85:505–517.
- Thiemann, G. W., S. J. Iverson, and I. Stirling. 2006. Seasonal, sexual and anatomical variability in the adipose tissue of polar bears (*Ursus maritimus*). *Journal of Zoology, London* 269:65–76.
- Thiemann, G. W., S. J. Iverson, and I. Stirling. 2007b. Variability in the blubber fatty acid composition of ringed seals (*Phoca hispida*) across the Canadian Arctic. *Marine Mammal Science* 23:241–261.
- Thiemann, G. W., S. J. Iverson, and I. Stirling. 2008. Variation in blubber fatty acid composition among marine mammals in the Canadian Arctic. *Marine Mammal Science* 24:91–111.
- Wielgus, R. B., and F. L. Bunnell. 1995. Tests of hypotheses for sexual segregation in grizzly bears. *Journal of Wildlife Management* 59:552–560.

APPENDIX A

A table summarizing the bear subpopulation distribution of samples from independent-age (≥ 2.5 yr) polar bears collected across the Canadian Arctic from 1972 to 2004 and used to examine interannual changes in diets (*Ecological Archives* M078-024-A1).

APPENDIX B

A table reporting fatty-acid composition and major lipid classes of the adipose tissue of all 1488 polar bears sampled between 1999 and 2004 (*Ecological Archives* M078-024-A2).

APPENDIX C

A table listing prey species and locations, and the number of prey blubber samples used to generate QFASA estimates of polar bear diets (*Ecological Archives* M078-024-A3).

APPENDIX D

A table and figure presenting calibration coefficients for polar bears derived from captive feeding studies on mink (*Mustela vison*) (*Ecological Archives* M078-024-A24).