

Variation in winter diet of southern Beaufort Sea polar bears inferred from stable isotope analysis

T.W. Bentzen, E.H. Follmann, S.C. Amstrup, G.S. York, M.J. Wooller, and T.M. O'Hara

Abstract: Ringed seals (*Phoca hispida* Schreber, 1775 = *Pusa hispida* (Schreber, 1775)) and bearded seals (*Erignathus barbatus* (Erxleben, 1777)) represent the majority of the polar bear (*Ursus maritimus* Phipps, 1774) annual diet. However, remains of lower trophic level bowhead whales (*Balaena mysticetus* L., 1758) are available in the southern Beaufort Sea and their dietary contribution to polar bears has been unknown. We used stable isotope ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$, $^{15}\text{N}/^{14}\text{N}$, and $\delta^{15}\text{N}$) analysis to determine the diet composition of polar bears sampled along Alaska's Beaufort Sea coast in March and April 2003 and 2004. The mean $\delta^{15}\text{N}$ values of polar bear blood cells were 19.5‰ (SD = 0.7‰) in 2003 and 19.9‰ (SD = 0.7‰) in 2004. Mixing models indicated bowhead whales composed 11%–26% (95% CI) of the diets of sampled polar bears in 2003, and 0%–14% (95% CI) in 2004. This suggests significant variability in the proportion of lower trophic level prey in polar bear diets among individuals and between years. Polar bears depend on sea ice for hunting seals, and the temporal and spatial availabilities of sea ice are projected to decline. Consumption of low trophic level foods documented here suggests bears may increasingly scavenge such foods in the future.

Résumé : Les phoques marbrés (*Phoca hispida* Schreber, 1775 = *Pusa hispida* (Schreber, 1775)) et les phoques barbus (*Erignathus barbatus* (Erxleben, 1777)) constituent la plus grande partie du régime alimentaire annuel de l'ours polaire (*Ursus maritimus* Phipps, 1774). Il y a cependant des restes de baleines franches boréales (*Balaena mysticetus* L., 1758), un animal de niveau trophique inférieur, disponibles dans le sud de la mer de Beaufort; leur contribution au régime des ours polaires est inconnue. Nous avons utilisé une analyse des isotopes stables ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$, $^{15}\text{N}/^{14}\text{N}$ et $\delta^{15}\text{N}$) afin de déterminer la composition du régime alimentaire des ours polaires dans la mer de Beaufort, le long de la côte d'Alaska, en mars et avril 2003 et 2004. Les valeurs moyennes de $\delta^{15}\text{N}$ des érythrocytes d'ours polaires étaient de 19,5 ‰ (ET = 0,7 ‰) en 2003 et de 19,9 ‰ (ET = 0,7 ‰) en 2004. Des modèles de mélange indiquent que les baleines franches boréales représentent 11 % – 26 % (IC de 95 %) du régime alimentaire des ours polaires échantillonnés en 2003 et 0 % – 14 % (IC de 95 %) en 2004. Cela révèle une importante variation entre les individus et les années dans la proportion des proies de niveau trophique inférieur dans le régime alimentaire des ours polaires. Les ours polaires utilisent la banquise pour la chasse au phoque et on prédit une diminution de la disponibilité temporelle et spatiale de la banquise dans le futur. La consommation de nourriture de niveau trophique inférieur observée ici laisse croire que les ours risquent de plus en plus de se servir de telles charognes dans l'avenir.

[Traduit par la Rédaction]

Introduction

Polar bears (*Ursus maritimus* Phipps, 1774) are a top carnivore in the Arctic marine ecosystem. They hunt and scavenge opportunistically and have been directly observed feeding on a variety of marine mammals (Stirling and Archibald 1977; Lowry et al. 1987; Calvert and Stirling 1990; Rugh and Shelden 1993; Derocher et al. 2002). Polar bear habitat is predicted to change as a warming Arctic reduces the spatial and temporal availabilities of sea ice (Holland et al. 2006). A detailed understanding of polar bear diet is necessary to understand the ecological impacts of possible habitat changes. Polar bears depend upon sea ice for hunting, which is a highly variable habitat and is sub-

ject to change owing to shifts in weather conditions and water currents. Individuals frequently move over 50 km per day, over ice, water, and along shorelines, in search of prey and of optimal hunting conditions near open leads and in active zones of the polar ice pack (Garner et al. 1990; Amstrup et al. 2000; Ferguson et al. 2000; Durner et al. 2004). These relatively shallow, nearshore waters (25–100 m) are among the most productive areas in the Arctic marine ecosystem and support a variety of prey species that are available to polar bears (Stirling and Derocher 1993; Sakshaug et al. 1994).

Ringed seals (*Phoca hispida* Schreber, 1775 = *Pusa hispida* (Schreber, 1775)) are found throughout the range of the polar bear and represent the majority of their annual

Received 9 October 2006. Accepted 13 April 2007. Published on the NRC Research Press Web site at cjz.nrc.ca on 26 May 2007.

T.W. Bentzen.¹ Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.
E.H. Follmann and T.M. O'Hara. Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.
S.C. Amstrup and G.S. York. US Geological Survey, Alaska Science Center, Anchorage, AK 99503, USA.
M.J. Wooller. Institute of Marine Sciences, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.

¹Corresponding author (e-mail: fstwb@uaf.edu).

diet (Lønø 1970; Smith 1980; Gjertz and Lydersen 1986; Derocher et al. 2002). Polar bears are highly efficient and specialized predators of ringed seals throughout the year (Stirling and Archibald 1977; Stirling 2002) and prey heavily on pups in their first spring (Hammill and Smith 1991; Stirling and Øritsland 1995; Wiig et al. 1999; Stirling 2002).

Bearded seals (*Erignathus barbatus* (Erxleben, 1777)) are also available to polar bears year-round in the southern Beaufort Sea. Adult bearded seals are significantly larger than ringed seals, thereby providing a greater biomass (per animal) than ringed seals. In Svalbard, Derocher et al. (2002) compiled data from 17 years of tracking bears by helicopter and reported the numerical composition of kills. Polar bear kills were dominated by ringed seal (75%), followed by bearded seal (16%), and harp seal (*Pagophilus groenlandicus* (Erxleben, 1777); 9%). Examination of stomach contents from hunter-killed bears in the same area reported similar proportions of ringed and bearded seals in the diet of Svalbard polar bears (Lønø 1970). Of polar bear kills observed while tracking in the Alaskan portion of the southern Beaufort Sea, ringed seals predominate, although bearded seal carcasses are frequently observed (S.C. Amstrup, personal communication (2005)).

In addition to ringed and bearded seals, polar bears along Alaska's Beaufort Sea coast, and elsewhere in the Arctic, have been observed consuming beluga whales (*Delphinapterus leucas* (Pallas, 1776)) and walrus (*Odobenus rosmarus* (L., 1758)) (Lowry et al. 1987; Calvert and Stirling 1990; Smith and Sjare 1990; Rugh and Sheldon 1993). Both walrus and beluga are migratory species that overwinter in the Bering Sea (Sease and Chapman 1988; Hazard 1988), but may be accessible to Beaufort Sea polar bears on a limited basis. Beach-cast walrus carcasses have been observed along the Beaufort Sea coast in June and July, but fewer than five carcasses were recorded during aerial surveys conducted in 1995 and 1997 (Kalxdorff 1998). Winter availability of beluga whales and walrus to Beaufort Sea polar bears is likely limited. However, the overall contribution of these species to polar bear diets remains unclear.

When available, polar bears will scavenge on the remains of bowhead whales (*Balaena mysticetus* L., 1758). Along Alaska's Beaufort Sea coast, bowhead whale carcasses are utilized by scavenging polar bears following the traditional hunt of the Inupiat people (Miller et al. 2004). These communities have harvested bowhead whales for generations (Reeves 2002), and currently, the Alaska Eskimo Whaling Commission, with permission of the International Whaling Commission, allows an annual quota of whales to be harvested. Among the three whaling communities along Alaska's portion of the Beaufort Sea, 26 whales were landed in fall 2002 and 13 whales were landed in fall 2003 (Suydam et al. 2002; Suydam et al. 2003). Following these successful hunts, polar bear aggregations of up to 60 individuals were reported around bowhead harvest sites (Miller et al. 2004). After butchering, the bowhead remains frequently left on shore or on floating sea ice are accessible to scavengers. Because of the bowhead's large mean body size, single carcasses may represent a massive food source for many scavengers (George et al. 2005). Whales struck by hunters but subsequently lost, beach-cast whales, those frozen in the ice, and whales stranding after natural deaths may also be-

come available to polar bears. Similar aggregations of polar bears were noted feeding at stranded beluga and sperm whale (*Physeter catodon* L., 1758) carcasses around Svalbard by Derocher et al. (2002).

Gray whales (*Eschrichtius robustus* (Lilljeborg, 1861)) annually migrate to feed in the coastal shoal habitats of the Alaskan Arctic from July through October (Moore et al. 2000). Although there is no official subsistence hunt for gray whales in Alaska, a limited number of beach-cast gray whales do occur along the coast in the summer and autumn months (J. George, North Slope Borough – Department of Wildlife Management, unpublished data (2004)). These whales present another potential low trophic level dietary source for polar bears along Alaska's Beaufort Sea coast; however, the numbers available in winter are likely low.

Most dietary studies of polar bears have been observations of killed prey (Stirling and Archibald 1977; Hammill and Smith 1991; Derocher et al. 2002). The relative importance of each of the potential prey species in the diet of polar bears is poorly understood and likely varies with sex, age, location, time of year, and fluctuations in annual availability. Stable isotope analyses of carbon ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$, $\delta^{15}\text{N}$) have been used as a tool for evaluating trophic relationships in the Arctic marine food web (Hobson and Welch 1992; Atwell et al. 1998; Pauly et al. 1998; Hoekstra et al. 2002; Dehn et al. 2005, 2006). In particular, $\delta^{15}\text{N}$ composition of an organism has been used as an indicator of its relative trophic position. There is generally a 3‰–5‰ increase in $\delta^{15}\text{N}$ values with each trophic transfer (Hobson and Welch 1992; Kelly 2000), which provides an integrated measure of the trophic position of an organism over time (Atwell et al. 1998; Pond and Gilmour 1997). In addition to measuring between-species trophic relationships in the Arctic marine food web, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values have been used to trace dietary history and nutritional ecology within populations, as well as movements between geographically distinct ecosystems (Abend and Smith 1995; Hilderbrand et al. 1996; Pond and Gilmour 1997; Hobson and Schell 1998; Bowen et al. 2005). By using stable isotopes of two elements and mass balance equations, it is possible to estimate the proportions of three isotopically distinct prey items that may make up the diet of the predator (Hilderbrand et al. 1996; Hilderbrand et al. 1999; Phillips and Gregg 2001; Ben-David et al. 2004).

In this study, we used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses to describe the feeding ecology of Beaufort Sea polar bears, focusing on three known fall and winter foods (i.e., ringed seals, bearded seals, and remains of bowhead whales). Ringed and bearded seals are both high trophic level predators with mixed diets consisting of varying proportions of fish and marine invertebrates (Lowry et al. 1980; Dehn et al. 2005). Although both ringed and bearded seals occupy a similar trophic level as measured by $\delta^{15}\text{N}$, their mean $\delta^{13}\text{C}$ signatures differ by approximately 1.5‰ (Hoekstra et al. 2002; Dehn et al. 2005). Because bowhead whale diet is composed primarily of pelagic zooplankton, they occupy a significantly lower trophic position than that of piscivorous marine mammals such as ringed seals (Hobson and Welch 1992; Lowry 1993; Pauly et al. 1998). Hoekstra et al. (2002) indicated that bowhead whales are depleted by about 3.0‰ in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ relative to ringed seals. Therefore, polar bears that scavenge

bowhead whale remains consume a diet with relatively lower $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values than do bears that feed almost exclusively on seals. Differences in the stable isotope signatures of individual polar bears may make it possible to better quantify the relative contributions of seals and lower trophic level prey items, such as bowhead whale, in the winter diet of southern Beaufort Sea polar bears. Because the temporal and spatial availabilities of sea ice in the Beaufort Sea are projected to be reduced (Holland et al. 2006), availability of seal prey may also decrease. Baseline understandings of the current diet of polar bears will provide a necessary measure against which future diets of Beaufort Sea polar bears can be compared.

Methods

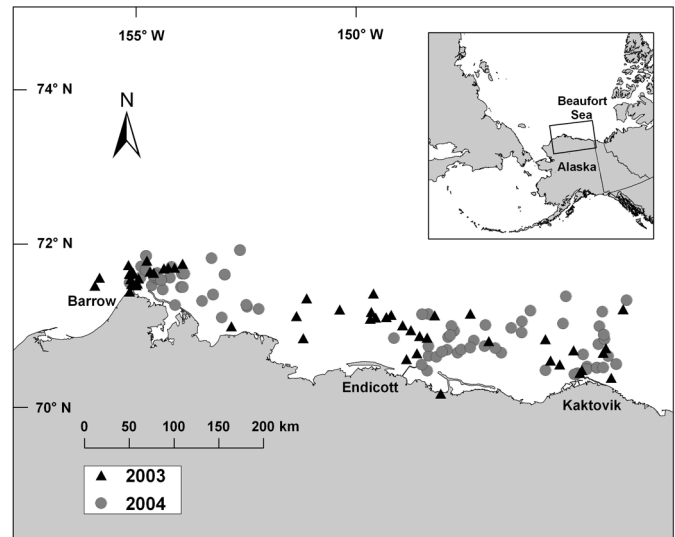
Study area

The southern Beaufort Sea population of polar bears inhabits a region extending along the north coast of Alaska and Canada from Point Lay at 163°W to Cape Perry in Amundsen Gulf at 125°W and extending north along Banks Island to Prince Patrick Island, Canada (Bethke et al. 1996; Paetkau et al. 1999; Amstrup et al. 2000). Although individual bears typically remain in one population, there is travel between populations and considerable geographic overlap among bears from adjacent populations, which is an important factor near Pt. Barrow where individual bears have about a 50% chance of originating from the southern Beaufort or Chukchi sea stock (Amstrup et al. 2004). Farther east, along Alaska's Beaufort Sea coast, mixing between populations becomes less pronounced (Amstrup et al. 2005). Polar bears in the southern Beaufort Sea remain primarily on the ice throughout the year (Garner et al. 1990; Scribner et al. 1997; Amstrup et al. 2000), congregating along ice edges (Durner et al. 2004). Leads of open water are frequently found throughout the year, and sea-ice coverage varies from continuous to approximately 50% open water in late summer (Durner et al. 2004).

Polar bear captures

Polar bear studies were conducted from Barrow ($71^\circ16'\text{N}$, $156^\circ47'\text{W}$), Endicott Island ($70^\circ18'\text{N}$, $147^\circ52'\text{W}$), and Kaktovik ($70^\circ08'\text{N}$, $143^\circ34'\text{W}$), Alaska. Bears were captured up to 80 km offshore in the area between Barrow and Demarcation Point ($69^\circ70'\text{N}$, $141^\circ00'\text{W}$) (Fig. 1). Polar bears were captured by injecting intramuscular immobilizing drugs contained in projectile syringes fired from a helicopter using Cap-chur equipment (Palmer Chemical Co., Douglasville, Georgia), with a 200 mg/mL solution of tiletamine hydrochloride and zolazepam hydrochloride (Telazol®; Warner-Lambert Co., Fort Dodge, Iowa) (Stirling et al. 1989; Amstrup et al. 2000, 2001). Sampling occurred from March to May 2003 and 2004. All capture procedures were reviewed and approved by independent animal care and use committees. Sex was determined, mass was estimated (Durner and Amstrup 1996), and physical condition was visually assessed for all captured bears. Newly captured bears were marked with a tattoo and an ear tag, and a vestigial premolar was extracted to determine age by counting cementum annuli (Calvert and Ramsay 1998).

Fig. 1. Northern Alaska and the southern Beaufort Sea, showing capture locations of all polar bears (*Ursus maritimus*) and the locations of Barrow, Endicott, and Kaktovik from which polar bear studies were conducted in spring 2003 and spring 2004.



Sample collection and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ analysis

Blood (5 mL) was collected from the femoral vein or artery of 43 polar bears (19 females and 24 males) in spring 2003 and of 96 bears (55 females and 41 males) in 2004. Vacutainers (without anticoagulant) of whole blood were centrifuged at 3000 rev/min (RCF = 700g) for 5 min, using a clinical IEC centra CL2 centrifuge, and packed blood cells were frozen at -20°C for analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

Stable isotope analysis was conducted at the Alaska Stable Isotope Facility at the University of Alaska Fairbanks. All samples were freeze-dried and homogenized into a fine powder. Using a Sartorius M2P electronic microbalance, aliquots of 0.2–0.4 mg (dry mass) of the tissue were measured into a tin capsule and analyzed for stable nitrogen and carbon isotope ratios using a Carlo Erba NC 2500 elemental analyzer coupled to a Finnigan Delta+ continuous-flow isotope-ratio mass spectrometer via a ConFlo III for continuous-flow measurements. Stable isotope compositions are reported using the standard δ notation and are referenced to Vienna PeeDee Belemnite and air for carbon and nitrogen, respectively. For quality assurance and control, all but three samples were analyzed in duplicate. The mean isotope value of the duplicate samples was then calculated for each bear and used in all further diet analysis. Analysis of a peptone standard (Sigma Chemical Co., Highland, Illinois) during the sample run for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ gave analytical precision of $\pm 0.1\text{‰}$ and $\pm 0.2\text{‰}$, respectively.

Statistical analysis

General linear models (GLM) were used to examine relationships between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and age, sex, mass, and location of capture. First, a two-factor ANOVA was used to detect any effects of sex, capture location, or their interaction on the stable isotope signatures. The assumptions of equal variance and normality of the residuals were assessed (Shapiro–Wilk test, $P > 0.05$). If the distributions of isotope values were not normally distributed within one or

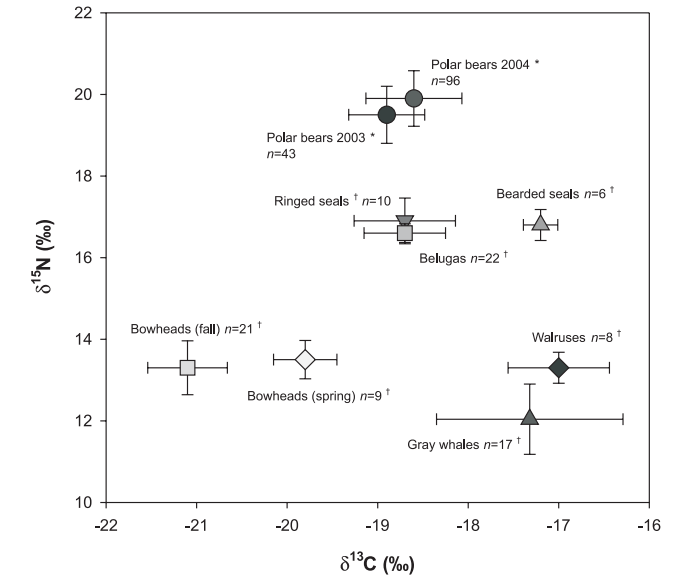
more groups, a two-factor ANOVA was run on the normal scores and the results were compared with the results from the ANOVA on the raw isotope data and examined for differences (Conover 1999). In all cases ANOVA results on the raw data are presented. Because age and mass were highly correlated in 2003 ($r = 0.573$, $P < 0.0001$, $n = 41$) and 2004 ($r = 0.539$, $P < 0.0001$, $n = 90$), a multiple regression model could not be used to test for the effects of age and mass on isotope signatures. Therefore, simple linear regression models were used to compare isotope signatures with the variables age and mass independently. All analyses were conducted using SAS[®] version 8.0 (SAS Institute Inc. 1990), with α set at 0.05.

To estimate prey composition in the polar bear diet, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were used from blood (packed cells) of all polar bears ($n = 139$). Stable isotope data published by Hoekstra et al. (2002) on muscle samples from bowhead whales collected during the fall whale harvest at Barrow ($n = 21$), as well as ringed seals ($n = 33$) and bearded seals ($n = 6$) from Barrow, were used in this analysis (Fig. 2). All seal and whale isotope values were obtained from muscle samples collected by subsistence hunters.

A linear mass balance equation was used for the two-element three-source mixing model to estimate relative contributions of each of three isotopically distinct fall and winter food sources (Robbins et al. 2002). This incorporated bearded seals, ringed seals, and bowhead whales into diet estimates for all polar bears and allowed comparison of polar bear diets between years. The IsoError model (Phillips and Gregg 2001) was used to calculate confidence intervals (CIs) around the diet estimates of the three-source mixing models. The IsoError model takes into account variability in both polar bears' isotopic signatures and the variability in stable isotope signatures inherent within each of three primary prey species. This allows us to represent diet ranges based on 95% CI instead of relying on the mean values, which may be misleading because they do not fully incorporate natural variability in feeding ecology among individual animals.

Predicted $\delta^{15}\text{N}$ fractionation rates from diet to polar bear blood were calculated using the equation published by Hilderbrand et al. (1996) for use in black bears (*Ursus americanus* Pallas, 1780), which scales the fractionation rate to the $\delta^{15}\text{N}$ values of the prey consumed. The calculated fractionation rates varied from $+3.2\text{‰}$ $\delta^{15}\text{N}$ for ringed and bearded seals to $+3.5\text{‰}$ $\delta^{15}\text{N}$ for bowhead whales. Hilderbrand et al. (1996) reported that blood cells and muscle behaved similarly in captive mice, rabbits, and black bears. As these are the only data available for any bear species maintained on a known diet, it was considered the most appropriate for the polar bear models. In blood and muscle, $\delta^{13}\text{C}$ values closely represent the food type consumed and change little with trophic transfer (Tieszen et al. 1983; Peterson and Fry 1987; Klaassen et al. 2004). Trophic enrichment of $\delta^{13}\text{C}$ is very likely $<1.0\text{‰}$ per step, and most studies indicate rates between $+0.0\text{‰}$ and $+0.5\text{‰}$ being appropriate for the fractionation from the diet to the cellular portions of blood in mammalian carnivores (Hobson et al. 1996; Roth and Hobson 2000; Ben-David and Schell 2001; Kurle and Worthy 2002). Data are presented for models using zero increase in $\delta^{13}\text{C}$ from the diet into the cellular portions of blood. Hilder-

brand et al. (1996) reported zero $\delta^{13}\text{C}$ fractionation into black bear blood for a diet with a $\delta^{13}\text{C}$ value between that of ringed seals and that of bearded seals (approximately -18.0‰). However, we recognize that this comparison has limitations, as polar bears are likely to consume little vegetation and have higher lipid content in the diet compared with black bears.



brand et al. (1996) reported zero $\delta^{13}\text{C}$ fractionation into black bear blood for a diet with a $\delta^{13}\text{C}$ value between that of ringed seals and that of bearded seals (approximately -18.0‰). However, we recognize that this comparison has limitations, as polar bears are likely to consume little vegetation and have higher lipid content in the diet compared with black bears.

Results

Polar bear stable isotope signatures varied significantly between 2003 and 2004 ($\delta^{15}\text{N}$: $|t| = 3.12$, $\text{df} = 137$, $P = 0.002$; $\delta^{13}\text{C}$: $|t| = 3.01$, $\text{df} = 137$, $P = 0.003$). Among the 43 polar bears sampled in spring of 2003, $\delta^{15}\text{N}$ values ranged from 18.1‰ to 20.6‰ ($19.5\text{‰} \pm 0.70\text{‰}$, mean \pm SD) and $\delta^{13}\text{C}$ values ranged from -19.5‰ to -17.5‰ ($-18.9\text{‰} \pm 0.42\text{‰}$) (Table 1, Fig. 3). Chemically derived trophic level of the polar bears, as calculated from the $\delta^{15}\text{N}$ values (Hoekstra et al. 2002), ranged from 4.2 to 4.9, with a mean of 4.6. Among the 96 polar bears sampled in 2004, $\delta^{15}\text{N}$ values ranged from 18.3‰ to 21.4‰ ($19.9\text{‰} \pm 0.68\text{‰}$) and $\delta^{13}\text{C}$ values ranged from -19.5‰ to -17.4‰ ($-18.6\text{‰} \pm 0.53\text{‰}$) (Fig. 4). Numerically, the range in trophic level among the 2004 polar bears was slightly broader than the range among 2003 polar bears. The calculated trophic level ranged from 4.2 to 5.0, with a mean of 4.7.

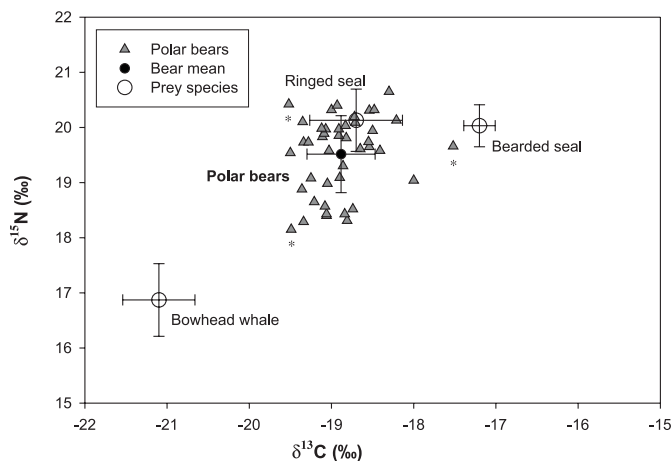
$\delta^{15}\text{N}$ isotope analysis

When bears sampled in 2003 were grouped by sex and capture location, $\delta^{15}\text{N}$ values departed significantly from a normal distribution (Shapiro–Wilk test, $P < 0.05$). Transformation of the $\delta^{15}\text{N}$ data did not improve normality. Therefore, we compared separate two-factor ANOVAs on the raw $\delta^{15}\text{N}$ data and on the normal scores of $\delta^{15}\text{N}$ (Conover 1999). Because the results of the ANOVAs did not differ substantially, we used the results de-

Table 1. Mean (SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, range, and sample size (n) of polar bear (*Ursus maritimus*) packed red blood cells sampled from three locations along Alaska's Beaufort Sea coast in spring 2003 and spring 2004.

Year and sex	Location	n	$\delta^{13}\text{C}$ (‰)	Max.	Min.	$\delta^{15}\text{N}$ (‰)	Max.	Min.
2003								
Females	Barrow	7	-19.0 ± 0.3	-18.6	-19.4	19.7 ± 0.6	20.4	18.9
	Endicott	8	-18.9 ± 0.4	-18.5	-19.3	19.7 ± 0.6	20.3	18.3
	Kaktovik	3	-19.2 ± 0.3	-18.9	-19.5	19.4 ± 0.9	20.4	18.6
Males	Barrow	9	-18.4 ± 0.4	-17.5	-18.8	19.5 ± 0.7	20.2	18.4
	Endicott	9	-19.0 ± 0.3	-18.5	-19.5	19.3 ± 0.9	20.3	18.2
	Kaktovik	7	-19.0 ± 0.4	-18.3	-19.5	19.6 ± 0.7	20.7	18.4
2004								
Females	Barrow	24	-18.3 ± 0.6	-17.4	-19.4	20.0 ± 0.7	21.4	18.8
	Endicott	16	-18.9 ± 0.5	-17.6	-19.5	20.1 ± 0.6	20.9	19.0
	Kaktovik	15	-18.8 ± 0.4	-18.1	-19.5	20.2 ± 0.7	21.0	19.1
Males	Barrow	17	-18.4 ± 0.5	-17.7	-19.3	19.6 ± 0.5	20.5	18.3
	Endicott	12	-18.8 ± 0.4	-17.9	-19.4	19.7 ± 0.5	20.5	18.8
	Kaktovik	12	-18.7 ± 0.4	-18.0	-19.2	19.8 ± 0.8	20.9	18.7

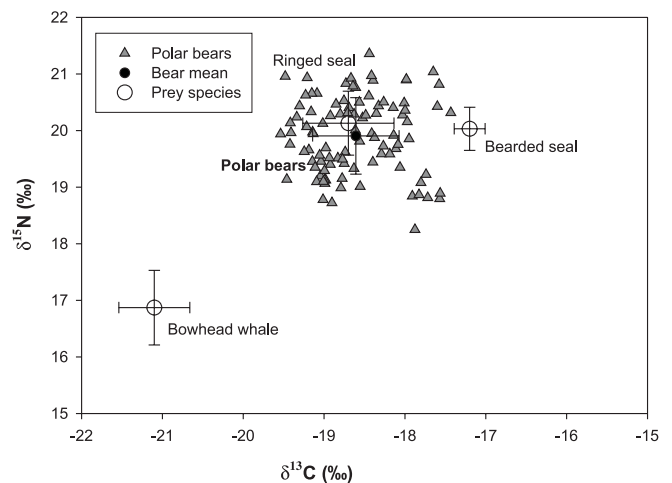
Fig. 3. Individual and mean (SD) stable isotope values of 43 polar bears captured in Alaska in spring 2003. Also shown are mean (SD) stable isotope values for ringed seal ($n = 33$), bearded seal ($n = 6$), and fall-captured bowhead whales ($n = 21$) adjusted one trophic level using the predicted fractionation rates of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ into cellular portions of polar bear blood. Asterisks indicate pairs of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values used for minimum and maximum ranges in diet estimates. Values for ringed seals, bearded seals, and fall-captured bowhead whales are from Hoekstra et al. (2002).



rived from the raw data. No significant differences in $\delta^{15}\text{N}$ values between sexes ($F_{[1,39]} = 1.14$, $P = 0.292$) or among the three capture locations ($F_{[2,39]} = 0.19$, $P = 0.830$) in 2003 were noted (Fig. 5). In 2004, sample size was larger and there were no significant departures from normality (Shapiro–Wilk test, $P > 0.05$). Females had about 0.4‰ higher $\delta^{15}\text{N}$ values than males ($F_{[1,92]} = 10.10$, $P = 0.002$). No significant effect of capture location on the $\delta^{15}\text{N}$ values was evident ($F_{[1,92]} = 0.42$, $P = 0.659$).

No significant differences in $\delta^{15}\text{N}$ values between females with cubs of the year and those without cubs were detected in 2003 ($F_{[1,41]} = 1.13$, $P = 0.307$) or in 2004 ($F_{[1,53]} = 1.01$, $P = 0.320$). $\delta^{15}\text{N}$ values did not vary significantly with the age of the polar bears ($F_{[1,41]} = 1.82$, $P = 0.185$) in 2003 or in 2004 ($F_{[1,93]} = 3.49$, $P = 0.065$). $\delta^{15}\text{N}$ values were also

Fig. 4. Individual and mean (SD) stable isotope values of 96 polar bears captured in Alaska in spring 2004. Also shown are mean (SD) stable isotope values for ringed seal ($n = 33$), bearded seal ($n = 6$), and fall-captured bowhead whales ($n = 21$) adjusted one trophic level using the predicted fractionation rates of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ into cellular portions of polar bear blood. Values for ringed seal, bearded seal, and fall-captured bowhead whales are from Hoekstra et al. (2002).



independent of bear mass in 2003 ($F_{[1,41]} = 3.06$, $P = 0.088$) and in 2004 ($F_{[1,89]} = 0.12$, $P = 0.727$).

$\delta^{13}\text{C}$ isotope analysis

We compared $\delta^{13}\text{C}$ values among capture locations and between sexes using a two-way ANOVA. There were no departures from normality for the residuals (Shapiro–Wilk test, $P > 0.05$). In 2003, $\delta^{13}\text{C}$ values did not differ significantly between sexes ($F_{[1,37]} = 3.64$, $P = 0.064$). However, $\delta^{13}\text{C}$ values did vary by capture location ($F_{[2,37]} = 3.30$, $P = 0.048$) and by sex \times capture location interaction ($F_{[2,37]} = 4.40$, $P = 0.019$) (Fig. 6). This variation was driven by a 0.6‰ difference between the mean $\delta^{13}\text{C}$ values of males ($n = 8$) and of females ($n = 7$) sampled near Barrow in

Fig. 5. Mean (SE) $\delta^{15}\text{N}$ values of packed red blood cells from polar bears captured in Alaska in spring 2003 (a) and in spring 2004 (b), separated by sex and capture location. Letters indicate statistically significant differences between sexes ($P < 0.05$).

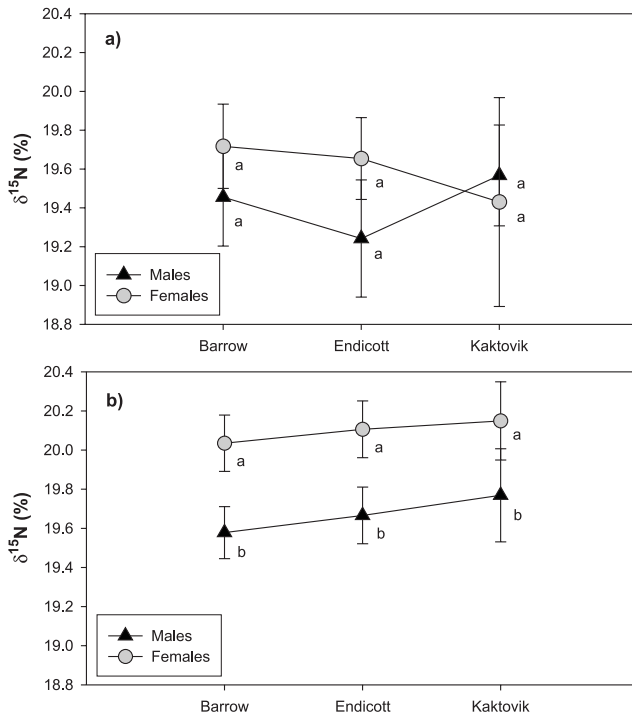
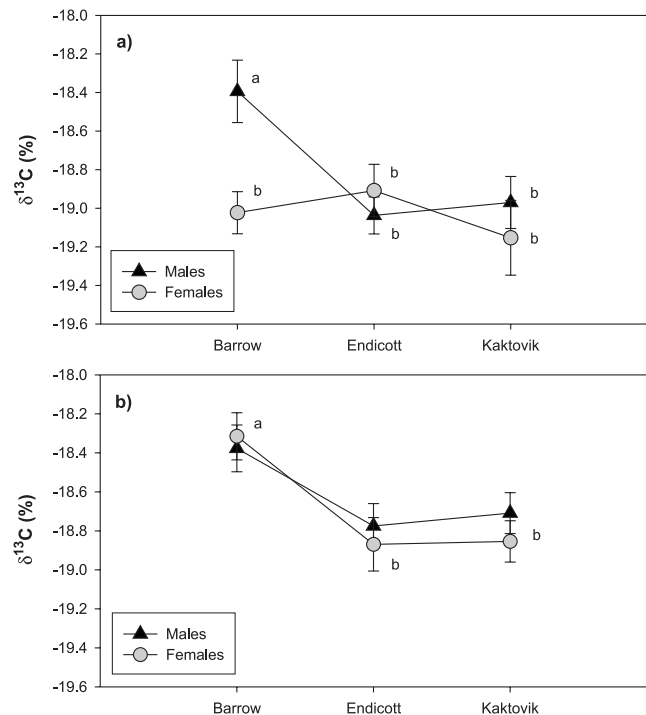


Fig. 6. Mean (SE) $\delta^{13}\text{C}$ values of packed red blood cells from polar bears captured in Alaska in spring 2003 (a) and in spring 2004 (b), separated by sex and capture location. Letters indicate statistically significant differences among locations ($P < 0.05$).



2003. In 2004, $\delta^{13}\text{C}$ values varied significantly by location; the $\delta^{13}\text{C}$ signature of polar bears collected from Barrow was 0.5‰ greater than that of polar bears sampled farther east ($F_{[2,92]} = 10.67$, $P < 0.005$). $\delta^{13}\text{C}$ values did not differ significantly between sexes in 2004 ($F_{[1,92]} = 0.16$, $P = 0.687$).

$\delta^{13}\text{C}$ values did not vary significantly with bear age in 2003 ($F_{[1,41]} = 3.74$, $P = 0.060$) or in 2004 ($F_{[1,93]} = 0.02$, $P = 0.894$) when sex and capture location were pooled. $\delta^{13}\text{C}$ values varied significantly with polar bear mass ($F_{[1,41]} = 7.70$, $P = 0.0085$). However, when bears were separated by sex, $\delta^{13}\text{C}$ values were not significantly correlated with mass in males ($F_{[1,22]} = 3.70$, $P = 0.068$) or in females ($F_{[1,17]} = 1.06$, $P = 0.319$). In 2004, $\delta^{13}\text{C}$ values did not vary significantly with polar bear mass ($F_{[1,89]} = 2.46$, $P = 0.120$).

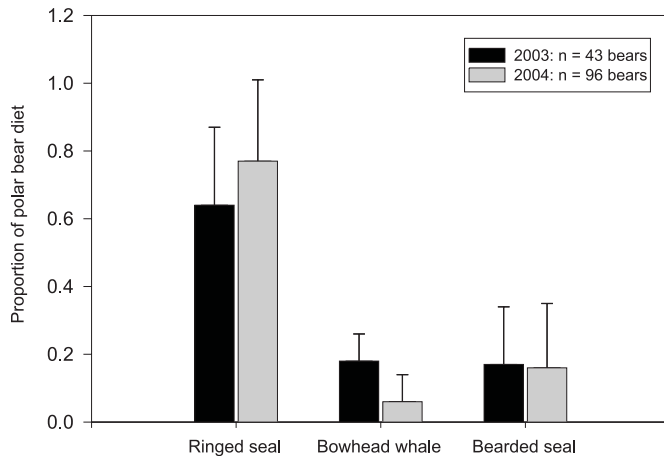
Mixing models

The IsoError model (Phillips and Gregg 2001) was used to calculate the proportional inputs of ringed seals, bearded seals, and bowhead whales, and to explain variation in the estimates of mean diet stemming from both the variability among individual polar bears and the variability inherent in the three dietary sources. The IsoError models produce a range of possible dietary proportions based on the variability within the diet sources and variability among polar bears. In 2003, the model indicated that diets consisted primarily of ringed seals, which represented 42%–87% (95% CI), with a mean of 64% of the overall diet (Fig. 7). In this model, bearded seals composed a possible range of 1%–34% (95% CI), with mean point estimate of 17% of the diet. Bowhead whales represented a similar dietary proportion, with a range of 11%–26% (95% CI) and a mean estimate of 18%. Results

from 2004 indicate that there may have been a nearly complete dependence on seals for many bears. Ringed seals were estimated at 53%–100% (95% CI), with a mean of 77% of the average polar bear diet, while bearded seals were estimated at 0%–35% (95% CI), with a mean of 16% of the average polar bear diet. The relative mean contribution of bowhead whales was low, with a range of 0%–14% (95% CI) and a mean estimate of 6% of the diet.

In both years, the large range in isotope values suggested wide variation in winter diets among individuals (Fig. 3). Point estimates using the IsoError model for maximum and minimum pairs of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values produce a range in proportional estimates for ringed seals as prey from 0% to 100% among individual polar bears. The extreme estimates for bowhead whales as food for individual polar bears ranged from 0% to 59%. Although the mean estimates for bearded seal consumption were low, individual bears may have consumed a high proportion of bearded seals, as the range between minimum and maximum estimates for contribution of bearded seal to individual diet was enormous, from 0% to 97%. These highly variable estimates of dietary proportions illustrate the sensitivity of the IsoError model to accurate prey data and accurate fractionation rates. Small degrees of uncertainty in isotopic fractionation of prey values into polar bear blood cells can produce widely differing diet estimates and likely introduced some uncertainty in our model results. However, all models indicate the dominance of seals, with lower trophic level prey generally representing a much smaller proportion of most polar bear diets.

Fig. 7. Dietary proportions of the three food sources for southern Beaufort Sea polar bears in winter 2002–2003 and in winter 2003–2004. All means were calculated using the IsoError model (Phillips and Gregg 2001), which includes 95% confidence intervals around all diet estimates.



Discussion

Diet composition

Ice seals (i.e., ringed and bearded seals) formed the majority of the winter diet of polar bears in the southern Beaufort Sea. In both years of the study, our mixing models support evidence that ringed seals were the primary prey source (Stirling and Archibald 1977; Stirling and Øritsland 1995; Stirling and Lunn 1997; Derocher et al. 2002). In 2004, our estimates indicated an almost complete (53%–100%) dependence on ringed seals. Although up to 80% of ringed seals killed by polar bears may be young of the year (Stirling 2002), our study reinforces years of field observations which suggest that even during winter months, before seal pups are available, ringed seals are the primary prey species.

Although this study used stable isotope data obtained from muscle tissue of prey, numerous studies of polar bear feeding ecology have noted a dietary preference for fat (Stirling and McEwan 1975; Stirling and Øritsland 1995; Stirling 2002). Beaufort Sea polar bears, however, reach their lowest seasonal body mass in early spring (Durner and Amstrup 1996, Stirling 2002), and most seal carcasses are almost entirely consumed either by the bear that made the kill or by following bears and other scavengers (S.C. Amstrup, personal communication (2007)). Best (1985) found that polar bears in captivity consumed $20\% \pm 2\%$ meat and viscera when allowed to select between meats and blubber in the diet. Polar bears must satisfy dietary requirements for vitamins, protein, and calories and cannot rely solely on endogenous production to satisfy the necessary protein to calorie ratio (Best 1985; Kenny et al. 2004). Although bears in peak condition rely primarily on fat, the entire population may not be solely fat dependent. Portions of muscle and viscera are likely consumed with the blubber by many bears (Stirling and McEwan 1975; Stirling and Archibald 1977; Smith 1980; Best 1985). Similar to other studies unable to account for exact tissue proportions consumed by predators (Hilderbrand et al. 1996; Darimont and Reimchen 2002;

Hoekstra et al. 2003; Ben-David et al. 2004), we used polar bear blood cells and estimated the whole body stable isotope signature of ringed seals, bearded seals, and bowhead whales using muscle tissue.

Because of the very low nitrogen content of adipose tissue, it is likely that any differences in $\delta^{15}\text{N}$ isotope signatures between dietary fat (blubber) and muscle may have been masked by the much higher nitrogen content of muscle. Any difference in the $\delta^{15}\text{N}$ value of a diet based on fat or muscle may be small and difficult to detect. Although $\delta^{13}\text{C}$ values in ringed seal, bearded seal, and bowhead whale blubber are not well understood, previous studies have stressed that analyzing lipid-rich tissues can lead to significantly lower ($>4.0\text{‰}$) $\delta^{13}\text{C}$ ratios relative to muscle (Tieszen et al. 1983; Kurle and Worthy 2002). Because of this large range in $\delta^{13}\text{C}$ between muscle and blubber, we would expect to see noticeable differences between diets based entirely on fat or on lean tissue. The mean $\delta^{13}\text{C}$ signature of bears in both years of this study fell close to that of ringed seal muscle. Because $\delta^{13}\text{C}$ values change little with trophic enrichment (Kelly 2000), the signature of a polar bear diet based on seal fat should be depleted in $\delta^{13}\text{C}$ relative to seal muscle. Although fat is extremely important in polar bear diets and may be preferentially consumed by some individuals, our data support evidence that muscle and organ meat are important food sources for southern Beaufort Sea polar bears in winter.

Some bears apparently consumed a relatively large proportion of bearded seal biomass. For the sample population as a whole, however, bearded seals are predicted to compose $<18\%$ of the overall diet in either sample year. High proportions of fat in the diet may have resulted in relatively lower $\delta^{13}\text{C}$ values in polar bear blood than expected from a lean tissue diet. Uncertainty in the effect of the high fat diet on $\delta^{13}\text{C}$ enrichment in the polar bear likely reduced our ability to distinguish between similar dietary sources using only $\delta^{13}\text{C}$. This may have caused us to underestimate the diet proportion belonging to bearded seals, thus artificially inflating our ringed seal estimate. Using available data, it is not possible to adequately address a “fat correction” to end-member food sources. Our interpretation of bearded seal in polar bear diets must be viewed with caution, but estimates of lower trophic level prey based largely on $\delta^{15}\text{N}$ values are likely unaffected by varying ratios of blubber to other tissues. Further studies incorporating stable isotope analysis of seal fat, as well as muscle and organs, are needed to fully answer this question.

Significant variability in $\delta^{15}\text{N}$ values in polar bear blood between years may indicate varied use of lower trophic level prey. In 2003, our mixing model indicated that bowhead whales may have contributed 11%–26% (95% CI) of the diet from the sampled population. However, for the winter of 2003–2004, the predicted proportion of bowhead whales was lower 0%–14% (95% CI) and possibly represented a negligible portion of the overall diet. In addition to varied annual use at the level of the sample population, the wide range in $\delta^{15}\text{N}$ values further suggest variation in the consumption of bowhead whale tissue among individual bears.

Most bowhead whale carcasses are available to polar bears after the autumn whale hunt, starting in September in Kaktovik and continuing through mid-October in Barrow

(Suydam et al. 2002). In fall 2002, Barrow harvested 19 of the 26 whales captured along Alaska's Beaufort Sea coast. After the whales are butchered, polar bears have been recorded at their highest densities around bowhead carcasses in October preceding the formation of shore-fast ice. At this time, the lack of freshly formed near-shore ice may limit seal hunting in shallow waters where seal densities are thought to be highest (Amstrup et al. 2000). In September and October 2002, Miller et al. (2004) reported aggregations of up to 44 bears at the bowhead whale carcasses near the village of Kaktovik and 4 bears at the bowhead whale remains at Cross Island (70°29'N, 147°59'W). Similarly, up to 60 polar bears were observed at bowhead whale remains at Pt. Barrow in fall 2002, and throughout the winter, individual bears were observed feeding on the carcasses at Barrow and other sites where bowhead whale remains were available (J. George, North Slope Borough – Department of Wildlife Management, personal communication (2004)). Individual polar bears were observed continuing to visit these carcass remnants in March of the following spring (T. Bentzen, unpublished data (2003)).

Following the fall 2003 whale hunt, in which the community of Barrow took only 6 of the 13 whales landed by the three whaling communities along Alaska's Beaufort Sea coast, the remains of the whales were reportedly pushed into the water, making them unavailable to scavenging polar bears (J. George, North Slope Borough – Department of Wildlife Management, unpublished data (2003)). The combination of fewer whales taken and of changes in carcass management practices by the community greatly reduced the number of carcasses available to polar bears at Pt. Barrow that winter. Polar bear surveys in Fall 2003 recorded maximums of 61 and 6 bears at the Kaktovik and Cross Island bowhead whale remains, respectively (Miller et al. 2004). Reports for Barrow were much lower in 2003, possibly because of the lack of carcasses available to scavengers (J. George, North Slope Borough Polar Bear Patrol Program – Department of Wildlife Management, unpublished data (2003)).

Although bowhead whale remains from the subsistence harvest are likely the most abundant lower trophic level food source in winter for polar bears in the southern Beaufort Sea, struck-and-lost bowhead whales that may later strand, as well as bowhead whales and the occasional gray whales that die from natural causes, are also available to scavenging polar bears. Data suggest that stranded bowhead whales occur in small numbers along the Canadian portion of the southern Beaufort Sea. Pilots and community harvesters reported four stranded bowhead whales in 2003, and again in 2004, between Demarcation Point and Amundsen Gulf (L. Harwood, Fisheries and Oceans Canada, unpublished data (2006)).

Annual variation in the use of lower trophic level prey by polar bears predicted by our data are correlated with, and may have been affected by, the annual availability of bowhead whale carcasses for polar bears in the southern Beaufort Sea. However, many other undetermined factors such as ice conditions in fall and winter may have affected both their access to whale remains and their ability to hunt seals. Relative seal abundance and winter access to seals are also difficult to determine and may have played important roles

in polar bear use of lower trophic level prey during the study.

The IsoError model using two isotopes is limited to three diet sources, therefore Pacific walrus, gray whales, and beluga whales were not included in estimates of the winter diet, and our results may include undetermined amounts of these prey items in the diet. Some walrus carcasses may be available along the Beaufort Sea coast in winter, although their mass on a per individual basis is much lower than that of baleen whales. Data analyzed from muscle of eight walrus sampled at St. Lawrence Island indicated a trophic level similar to that of bowhead whale as measured by $\delta^{15}\text{N}$, although $\delta^{13}\text{C}$ values were approximately 3‰ higher (Bentzen 2006). The mean isotopic values of gray whale muscle (12.0‰ $\delta^{15}\text{N}$, -17.3‰ $\delta^{13}\text{C}$) captured in the Bering Sea are similar to that of walrus (13.3‰ $\delta^{15}\text{N}$, -17.0‰ $\delta^{13}\text{C}$) (Dehn et al. 2006). Although gray whales are not usually present in the Beaufort Sea in winter, the large average body size (11 m) (Varanasi et al. 1994) of a stranded gray whale carcass may provide scavengers with a food source into the winter months. Consumption of either of these potential lower trophic level prey species may have inflated the estimated proportion of bowhead whale in the diet.

The abundance and availability of beluga whales to polar bears in the southern Beaufort Sea vary greatly throughout the year but are limited in winter (Hazard 1988). Beluga whales feed at a similar trophic level to ringed and bearded seals. Both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of beluga whales differ <0.5‰ from those of ringed seals (Hoekstra et al. 2002), and we were unable to adequately differentiate them using these techniques. Beluga whales in the diet would have increased our estimate of higher trophic level prey, particularly ringed seal, but would not have affected the estimated contribution of lower trophic level prey.

Other potential dietary sources for southern Beaufort Sea polar bears, such as cannibalism on other bears (Derocher and Wiig 1999; Dyck and Daley 2002; Amstrup et al. 2006) and feeding on terrestrial mammals such as caribou (*Rangifer tarandus* (L., 1758)) (Lunn and Stirling 1985; Ramsay et al. 1991; Hobson and Stirling 1997; Brook and Richardson 2002), although possible are unlikely to have affected long-term tissue composition. The occurrence of both spotted seals (*Phoca largha* Pallas, 1811) and ribbon seals (*Histiophoca fasciata* (Zimmermann, 1783)) along the Beaufort Sea in late fall and winter is also low (Kelly 1988; Quakenbush 1988; Frost et al. 1993). We did not attempt to include any of these potential dietary sources in our models, but limited numbers may have been available to these bears.

Relative to non-denning females, Polischuk et al. (2001) reported a 2‰ increase in $\delta^{15}\text{N}$ values among female polar bears of western Hudson Bay that had fasted for 7–8 months and given birth to cubs. Because fasting polar bears rely entirely on endogenous reserves, they are effectively feeding at a higher trophic level (Atkinson et al. 1996). We hypothesized that the 0.4‰ difference observed between males and females in 2004 may have been driven by females with cubs of the year; these females had been fasting since entering dens in mid- to late October and therefore may have had higher $\delta^{15}\text{N}$ values. However, we found no effect of recent denning on trophic position of female bears in this study.

Population comparisons

We did not find significant differences in trophic level as measured by $\delta^{15}\text{N}$ between polar bears captured near Barrow compared with those captured farther east along Alaska's Beaufort Sea coast. However, beluga whale, gray whale, and walrus may be more important for polar bears in the Chukchi and Bering seas and are likely available there in higher numbers in fall and winter than in the Beaufort Sea (Hazard 1988; Sease and Chapman 1988; Moore et al. 2000). Because of the extensive overlap of the Beaufort and Chukchi polar bear populations around Pt. Barrow (Amstrup et al. 2004), it is likely that many of the bears sampled from Barrow were part of the Chukchi Sea population and may have had increased access to various lower trophic level prey in winter. Bowhead whale remains are not expected to be as available to polar bears in the Chukchi Sea because there is no regular fall harvest of whales in that area (Suydam et al. 2002, 2003).

In 2004, we detected significantly higher $\delta^{13}\text{C}$ values in polar bears sampled from Barrow than in those sampled near Endicott and Kaktovik. In 2003, only the males at Barrow were significantly higher than males from the other sites. This was possibly due to the smaller sample size of bears captured, which may have limited our ability to detect statistically significant differences in females among all three locations. Higher $\delta^{13}\text{C}$ values among bears captured near Barrow is likely caused by these individuals feeding to a greater extent in the Chukchi Sea. It is unlikely that this range of variation reflects major differences in feeding ecology and may be explained by location differences between the Beaufort, Chukchi, and Bering seas owing to the heterogeneity of stable carbon isotopes in zooplankton and the fish and mammals above them in the food chain. Relatively higher $\delta^{13}\text{C}$ signatures of the Bering and Chukchi seas have been observed in the $\delta^{13}\text{C}$ values of the baleen plates and muscle of bowhead whales at Barrow while migrating from the Bering to the Beaufort Sea (Hobson and Schell 1998; Hoekstra et al. 2002). This relationship has also been documented in the $\delta^{13}\text{C}$ values of ringed and bearded seals feeding near Barrow compared with those feeding farther east in the Canadian portion of the Beaufort Sea (Dehn et al. 2005).

Bowhead whale remains may represent a lower trophic level dietary source for polar bears in the southern Beaufort Sea that is unavailable to polar bear populations elsewhere in the Arctic. Although stranded bowhead whales from both eastern and western stocks do occur, it is unlikely that they provide polar bears in Baffin Bay and the Canadian archipelago with as large or consistent a source of food as does the indigenous subsistence hunt in Alaska. Comparisons of the stable isotope values among southern Beaufort Sea polar bears to published data from Canadian subpopulations reveal lower $\delta^{15}\text{N}$ values in blood plasma and muscle. The $\delta^{15}\text{N}$ values reported here were significantly lower than those in blood plasma samples of seven females with yearling cubs in Resolute ($|t| = 7.75$, $df = 7$, $P < 0.005$) (Polischuk et al. 2001). In addition, our $\delta^{15}\text{N}$ values averaged 1.3‰ lower than those of muscle samples obtained from three bears in Lancaster Sound ($|t| = 3.70$, $df = 2$, $P = 0.070$) (Hobson and Welch 1992); our inability to detect a difference may be due to the small sample size. Although the variation between polar bear populations may be due to the greater

availability of low trophic level prey such as bowhead whale in the southern Beaufort Sea, the dietary relationships are far from clear and the importance of alternative dietary sources such as walrus are not well understood for these populations. Additional uncertainty may have been added because of spatial differences in food-web values and because of variations in $\delta^{15}\text{N}$ fractionations between the cellular portions of blood, plasma, and muscle, which are not clearly understood for mammalian carnivores (Hilderbrand et al. 1996; Hobson et al. 1996; Roth and Hobson 2000). Differences in the timing of sampling and in the tissue types analyzed may add additional uncertainty when comparing populations.

Turnover rate

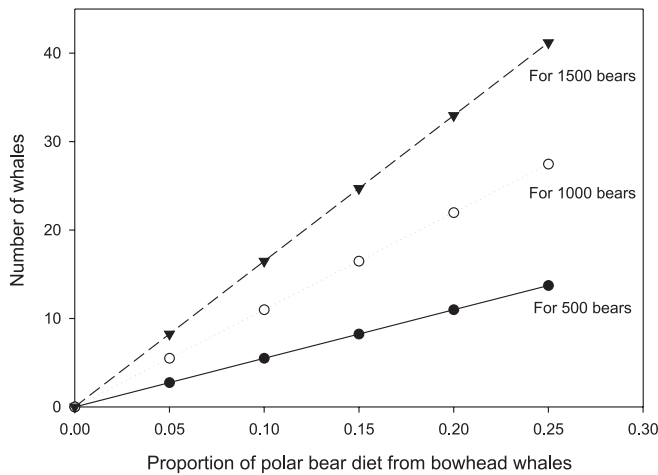
Knowledge about the turnover rate of nitrogen and carbon isotopes between tissues is important for understanding the scope of this study. Hilderbrand et al. (1996) found that isotope ratios of black bear red blood cells continued to change 40 days after a dietary shift. Studies using mammals varying from mink (*Mustela vison* Schreber, 1777) to long-nosed bandicoots (*Perameles nasuta* É. Geoffroy Saint-Hilaire, 1804) have produced estimates of the turnover of nitrogen and carbon in blood that vary from 3 to over 5 months (Tieszen et al. 1983; Ben-David 1996; Voigt et al. 2003; Klaassen et al. 2004). Our isotope ratios likely reflect nutrients incorporated into blood cells starting at a time period previous to collection, which is roughly two to three times longer than its isotopic half-life (Kurle and Worthy 2002) which we estimate to have been 1–2 months based on the results of Hilderbrand et al. (1996). This limits estimates of assimilated diet to a period of several months prior to sampling; therefore, our data are limited to inferences of polar bear diet accumulated primarily during the winter months.

Hunting success apparently decreases during winter, and polar bears usually reach their lowest mass in spring (Watts and Hansen 1987; Durner and Amstrup 1996). Because polar bears in the southern Beaufort Sea reach their peak mass in autumn (Durner and Amstrup 1996), the peak feeding period for polar bears apparently occurs in late summer and autumn. Observations also suggest that the highest numbers of bears are observed feeding on whale remains in late summer and autumn. Considerable time, therefore, may have elapsed between peak consumption of bowhead whale tissue and our sampling period. Nonetheless, the isotopic signature of bowhead whale, which was detectable in many bears, suggests some overwinter utilization of lower trophic level prey by polar bears in the southern Beaufort Sea.

Mass balance

We attempted to estimate the numbers of bowhead whale carcasses required to produce the diet proportions that we have suggested for polar bears along the Alaskan portion of the Beaufort Sea coast. These calculations make the assumption that bowhead whale compose between 0% and 25% of the annual diet during this study. Using estimates produced by Best (1985), which indicate an active adult polar bear requires 1825 kg of meat or 730 kg of blubber to meet yearly energetic requirements and assuming a mixed diet of meat, organs, and blubber, we used the value 1278 kg of food needed per bear per year. We then used the mass of an average bowhead whale landed at Barrow, Alaska (27 000 kg),

Fig. 8. Estimated numbers of bowhead whales, which is based on the entire carcass mass minus the mass of the skeleton, required to feed varying population levels of polar bears when bowhead whales compose between 0% and 25% of the total diet. $n_{\text{bowheads}} = n_{\text{bears}} \times [1\,278 \text{ kg}_{\text{food}} / (23\,274 \text{ kg}_{\text{bowhead}} / 2)] \times \text{proportion of diet}$.



and subtracted the estimated proportional mass of the skeleton (George et al. 2005). From this, we calculated an average mass available to bears from a whole bowhead whale carcass to be 23 274 kg, which we divided in half in an attempt to account for differences in consumable tissues between subsistence harvested whales and stranded whales entirely available to scavengers (Fig. 8). This indicates that fewer than 11 whale carcasses may be required to provide a chemically based trophic signature for 1000 polar bears at the 10% level for 1 year. This may underestimate the numbers of whales required because most subsistence-harvested whales will have had a large proportion of consumable tissues removed. However, it illustrates that relatively few whales may be required to influence the tissue composition of polar bears with respect to stable carbon and nitrogen isotope ratios.

Although the southern Beaufort Sea population of polar bears has been estimated to be between 1500 and 2500 individuals (Amstrup et al. 1986, 2001; Stirling 2002; Regehr et al. 2006), these include polar bears captured along both the Canadian and the Alaskan portions of the Beaufort Sea. Most polar bears sampled in this study were captured within 50 km of the coast, where densities are greatest. Our estimate of the dietary contribution of coastally associated lower trophic level prey may be an overestimation when applied to the entire population of southern Beaufort Sea polar bears. There appears to be two groups of polar bears near Svalbard (Mauritzen et al. 2001). One group primarily uses nearshore waters and coastal areas, while another uses offshore pack ice. Mauritzen et al. (2002) suggested that dietary differences between groups may have caused this difference. However, high seasonal movement rates between offshore and coastal areas are well documented in the southern Beaufort Sea (Amstrup et al. 2000, 2004), and similar divisions between space use and diet have not been recorded.

Conclusions

The $\delta^{15}\text{N}$ values from blood cells varied $>3\text{‰}$ among polar bears, suggesting that polar bears in the southern Beaufort Sea region feed on prey across a variety of trophic levels. Both the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values are lower than expected for a diet consisting exclusively of ice seals. Lower trophic level foods, such as bowhead whales, composed 11%–26% and 0%–14% of the winter diet of southern Beaufort Sea polar bears in 2003 and 2004, respectively. We observed dietary differences between the 2 years of the study and differences between the sexes in 2004 when females consumed less lower trophic level prey. These ranges may be consistent with observed movement patterns of radio-collared polar bears. Between 1985 and 2006, approximately 3% of radio-collared polar bears were confirmed to have scavenged at bowhead whale butchering sites (S.C. Amstrup, unpublished data (2005)), and some bears were known to visit butchering sites repeatedly within and among years. During that same period, however, nearly 18% of radio-collared bears were recorded near whale butchering sites. Given that Beaufort Sea polar bears may occasionally find naturally occurring carcasses of low trophic level marine mammals, our estimates seem reasonable and confirm that polar bears can take advantage of food sources at varied trophic levels. Annual variation in ice conditions, seal abundance, and the relative availability of subsistence-hunted bowhead whale remains, as well as polar bear sex and age class, apparently affect foraging patterns as estimated by stable isotope ratios.

Because polar bears depend on the ice surface for access to seals, which are their preferred prey, projected declines in spatial and temporal availabilities of ice in the Beaufort Sea region (Holland et al. 2006) could reduce future availability of seals. Seasonal ice retreats, thinning ice, and delayed ice formation may increase the numbers of polar bears on shore in autumn. These factors are likely to reduce access to preferred polar bear habitats (Stirling and Derocher 1993; Amstrup et al. 2000) where seals are most available and may increase polar bear use of human-mediated food sources such as carcasses of harvested bowhead whales. Our data confirm that bowhead whale carcasses, or other low trophic level foods, are already acceptable alternatives for some polar bears and the amount of lower trophic level prey in the diet likely varies greatly between individuals, between years, and between seasons. The dietary baselines established here will provide useful comparisons for diet studies conducted during what are forecasted to be very different future ice environments.

Acknowledgements

This project was initiated in support of US Minerals Management Service research priorities. Principal funding was provided by the USGS Outer Continental Shelf studies program and the Alaska Science Center. The USGS provided all polar bear samples used in our analysis in association with the Polar Bear Research Program and the Alaska Marine Mammal Tissue Archival Project. We thank the North Slope Borough Department of Wildlife Management, the Alaska Nanuq Commission, and the many people who helped collect data used in this study for their assistance. We thank N. Haubenstock and T. Howe at the University of

Alaska Fairbanks, Alaska Stable Isotope Facility, as well as the faculty and staff of the Institute of Arctic Biology and the Department of Biology and Wildlife at the University of Alaska Fairbanks. Particular thanks go to R. Bentzen, J.C. George, D. O'Brien, E. Murphy, P. Hoekstra, and M. Ben-David for their help with many questions and problems. Any use of trade names is for descriptive purposes only and does not imply endorsement of the US Government.

References

- Abend, A.G., and Smith, T.D. 1995. Differences in ratios of stable isotopes of nitrogen in long-finned pilot whales (*Globicephala melas*) in the western and eastern North Atlantic. *ICES J. Mar. Sci.* **52**: 837–841. doi:10.1006/jmsc.1995.0080.
- Amstrup, S.C., Stirling, I., and Lentfer, J. 1986. Size and trends of Alaskan polar bear populations. *Wildl. Soc. Bull.* **14**: 251–254.
- Amstrup, S.C., Durner, G.M., Stirling, I., Lunn, N.J., and Messier, F. 2000. Movements and distribution of polar bears in the Beaufort Sea. *Can. J. Zool.* **78**: 948–966. doi:10.1139/cjz-78-6-948.
- Amstrup, S.C., McDonald, T.L., and Stirling, I. 2001. Polar bears in the Beaufort Sea: a 30-year mark–recapture case history. *J. Agric. Biol. Environ. Stat.* **6**: 221–234.
- Amstrup, S.C., McDonald, T.L., and Durner, G.M. 2004. Using satellite radiotelemetry data to delineate and manage wildlife populations. *Wildl. Soc. Bull.* **32**: 661–679.
- Amstrup, S.C., Durner, G.M., Stirling, I., and McDonald, T.L. 2005. Allocating harvests among polar bear stocks in the Beaufort Sea. *Arctic*, **58**: 247–259.
- Amstrup, S.C., Stirling, I., Smith, T.S., Perham, C., and Thiemann, G.W. 2006. Recent observations of intraspecific predation and cannibalism among polar bears in the southern Beaufort Sea. *Polar Biol.* **29**: 997–1002. doi:10.1007/s00300-006-0142-5.
- Atkinson, S.N., Nelson, R.A., and Ramsay, M.A. 1996. Changes in the body composition of fasting polar bears (*Ursus maritimus*): the effect of relative fatness on protein conservation. *Physiol. Zool.* **69**: 304–316.
- Atwell, L., Hobson, K.A., and Welch, H.E. 1998. Biomagnification and bioaccumulation of mercury in an arctic marine food web: insights from stable nitrogen isotope analysis. *Can. J. Fish. Aquat. Sci.* **55**: 1114–1121. doi:10.1139/cjfas-55-5-1114.
- Ben-David, M. 1996. Seasonal diets of mink and martins: effects of spatial and temporal changes in resource abundance. Ph.D. thesis, Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks.
- Ben-David, M., and Schell, D. 2001. Mixing models in analyses of diet using multiple stable isotopes: a response. *Oecologia (Berl.)*, **127**: 180–184. doi:10.1007/s004420000570.
- Ben-David, M., Titus, K., and Beier, L.R. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia (Berl.)*, **138**: 465–474. doi:10.1007/s00442-003-1442-x. PMID:14673639.
- Bentzen, T.W. 2006. Winter feeding ecology and biomagnification of organochlorine contaminants in Alaskan polar bears. M.S. thesis, Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks.
- Best, R.C. 1985. Digestibility of ringed seals by the polar bear. *Can. J. Zool.* **63**: 1033–1036.
- Bethke, R., Taylor, M.K., Amstrup, S.C., and Messier, F. 1996. Population delineation of polar bears using satellite collar data. *Ecol. Appl.* **6**: 311–317. doi:10.2307/2269574.
- Bowen, G.J., Wassenaar, L.L., and Hobson, K.A. 2005. Global application of stable hydrogen and oxygen isotopes to wildlife for-
ensics. *Oecologia (Berl.)*, **143**: 337–348. doi:10.1007/s00442-004-1813-y. PMID:15726429.
- Brook, R.K., and Richardson, E.S. 2002. Observations of polar bear predatory behavior toward caribou. *Arctic*, **55**: 193–196.
- Calvert, W., and Ramsay, M.A. 1998. Evaluation of age determination of polar bears by counts of cementum growth layer groups. *Ursus*, **10**: 449–453.
- Calvert, W., and Stirling, I. 1990. Interactions between polar bears and overwintering walrus in the central Canadian High Arctic. *In Bears — Their Biology and Management: Proceedings of the Eighth International Conference on Bear Research and Management*, Victoria, B.C., 20–25 February 1989. Edited by L.M. Darling and W.R. Archibald. International Association for Bear Research and Management, Washington, D.C. pp. 351–356. [Available from Terry D. White, Department of Forestry, Wildlife, and Fisheries, The University of Tennessee, P.O. Box 1071, Knoxville, TN 37901-1071, USA; also refer to www.bearbiology.com]
- Conover, W.J. 1999. Practical nonparametric statistics. 3rd ed. John Wiley & Sons, Inc. New York.
- Darimont, C., and Reimchen, T. 2002. Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. *Can. J. Zool.* **80**: 1638–1642. doi:10.1139/z02-149.
- Dehn, L.-A., Sheffield, G.G., Follmann, E.H., Duffy, L.K., Thomas, D.L., Bratton, G.R., Taylor, R.J., and O'Hara, T.M. 2005. Trace elements in tissues of phocid seals harvested in the Alaskan and Canadian Arctic: influence of age and feeding ecology. *Can. J. Zool.* **83**: 726–746. doi:10.1139/z05-053.
- Dehn, L.-A., Follmann, E.H., Rosa, C., Duffy, L.K., Thomas, D.L., Bratton, G.R., Taylor, R.J., and O'Hara, T.M. 2006. Stable isotope and trace element status of subsistence-hunted bowhead and beluga whales in Alaska and gray whales in Chukotka. *Mar. Pollut. Bull.* **52**: 301–319. PMID:16216281.
- Derocher, A.E., and Wiig, Ø. 1999. Infanticide and cannibalism of juvenile polar bears (*Ursus maritimus*) in Svalbard. *Arctic*, **52**: 307–310.
- Derocher, A.E., Wiig, Ø., and Andersen, M. 2002. Diet composition of polar bears in Svalbard and the western Barents Sea. *Polar Biol.* **25**: 448–452.
- Durner, G.M., and Amstrup, S.C. 1996. Mass and body-dimension relationships of polar bears in northern Alaska. *Wildl. Soc. Bull.* **24**: 480–484.
- Durner, G.M., Amstrup, S.C., Neilson, R., and McDonald, T. 2004. The use of sea ice habitat by female polar bears in the Beaufort Sea. OCS study, MMS 2004-014, US Geological Survey, Alaska Science Center, Anchorage.
- Dyck, M.G., and Daley, K.J. 2002. Cannibalism of a yearling polar bear (*Ursus maritimus*) at Churchill, Canada. *Arctic*, **55**: 190–192.
- Ferguson, S.H., Taylor, M.K., and Messier, F. 2000. Influence of sea ice dynamics on habitat selection by polar bears. *Ecology*, **81**: 761–772. doi:10.2307/177375.
- Frost, K.J., Lowry, L.F., and Carroll, G. 1993. Beluga whale and spotted seal use of a coastal lagoon system in the northeastern Chukchi Sea. *Arctic*, **46**: 8–16.
- Garner, G.W., Knick, S.T., and Douglas, D.C. 1990. Seasonal movements of adult female polar bears in the Bering and Chukchi Seas. *In Bears — Their Biology and Management: Proceedings of the Eighth International Conference on Bear Research and Management*, Victoria, B.C., 20–25 February 1989. Edited by L.M. Darling and W.R. Archibald. International Association for Bear Research and Management, Washington, D.C. pp. 219–226. [Available from Terry D. White, Department of Forestry, Wildlife, and Fisheries, The University of Tennessee,

- P.O. Box 1071, Knoxville, TN 37901-1071, USA; also refer to www.bearbiology.com]
- George, J.C., Philo, L.M., Thompson, S., and Suydam, R. 2005. Approaches for estimating the body mass of bowhead whales (*Balaena mysticetus*) of the Bering Chukchi Beaufort Seas stock. North Slope Borough, Department of Wildlife Management, Barrow, Alaska.
- Gjertz, I., and Lydersen, C. 1986. Polar bear predation on ringed seals in the fast-ice of Hornsund, Svalbard. *Polar Res.* **4**: 65–68.
- Hammill, M.O., and Smith, T.G. 1991. The role of predation in the ecology of the ringed seal in Barrow Straight, Northwest Territories, Canada. *Mar. Mamm. Sci.* **7**: 123–135. doi:10.1111/j.1748-7692.1991.tb00559.x.
- Hazard, K. 1988. Beluga whale, *Delphinapterus leucas*. In Selected marine mammals of Alaska: species accounts with research and management recommendations. Edited by J.W. Lentfer. Marine Mammal Commission, Washington, D.C. pp. 195–235.
- Hilderbrand, G.V., Farley, S.D., Robbins, C.T., Hanley, T.A., Titus, K., and Servheen, C. 1996. Use of stable isotopes to determine diets of living and extinct bears. *Can. J. Zool.* **74**: 2080–2088.
- Hilderbrand, G.V., Schwartz, C.C., Robins, C.T., Jacoby, M.E., Hanley, T.A., Arthur, S.M., and Servheen, C. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Can. J. Zool.* **77**: 132–138. doi:10.1139/cjz-77-1-132.
- Hobson, K.A., and Schell, D.M. 1998. Stable carbon and nitrogen isotope patterns in baleen from eastern Arctic bowhead whales (*Balaena mysticetus*). *Can. J. Fish. Aquat. Sci.* **55**: 2601–2607. doi:10.1139/cjfas-55-12-2601.
- Hobson, K.A., and Stirling, I. 1997. Low variation in blood $\delta^{13}\text{C}$ among Hudson Bay polar bears: implications for metabolism and tracing terrestrial foraging. *Mar. Mamm. Sci.* **13**: 359–367. doi:10.1111/j.1748-7692.1997.tb00645.x.
- Hobson, K.A., and Welch, H.E. 1992. Determination of trophic relationships within a high arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar. Ecol. Prog. Ser.* **84**: 9–18.
- Hobson, K.A., Schell, D.M., Renouf, D., and Noseworthy, E. 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Can. J. Fish. Aquat. Sci.* **53**: 528–533. doi:10.1139/cjfas-53-3-528.
- Hoekstra, P.F., Dehn, L.-A., George, J.C., Solomon, K.R., Muir, D.C.G., and O'Hara, T.M. 2002. Trophic ecology of bowhead whales (*Balaena mysticetus*) compared with that of other arctic marine biota as interpreted from carbon-, nitrogen-, and sulfur-isotope signatures. *Can. J. Zool.* **80**: 223–231. doi:10.1139/z01-229.
- Hoekstra, P.F., Braune, B.M., O'Hara, T.M., Elkin, B., Solomon, K.R., and Muir, D.C.G. 2003. Organochlorine contaminant and stable isotope profiles in Arctic fox (*Alopex lagopus*) from the Alaskan and Canadian Arctic. *Environ. Pollut.* **122**: 423–433. doi:10.1016/S0269-7491(02)00310-X. PMID:12547532.
- Holland, M.M., Bitz, C.M., and Tremblay, B. 2006. Future abrupt reductions in the summer Arctic sea ice. *Geophys. Res. Lett.* **33**: L23503. doi:10.1029/2006GL028024.
- Kalxdorff, S.B. 1998. Distribution and abundance of marine mammal carcasses along beaches of the Bering, Chukchi, and Beaufort seas, Alaska, 1995–1997. OCS study, MMS 1998, U.S. Department of the Interior, Anchorage, Alaska.
- Kelly, B.P. 1988. Ribbon seal, *Phoca fasciata*. In Selected marine mammals of Alaska: species accounts with research and management recommendations. Edited by J.W. Lentfer. Marine Mammal Commission, Washington, D.C. pp. 195–235.
- Kelly, J.F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Can. J. Zool.* **78**: 1–27. doi:10.1139/cjz-78-1-1.
- Kenny, D.E., O'Hara, T.M., Chen, T.C., Lu, Z.R., Tian, X., and Holick, M.F. 2004. Vitamin D content in Alaskan Arctic zooplankton, fishes, and marine mammals. *Zoo Biol.* **23**: 33–43. doi:10.1002/zoo.10104.
- Klaassen, M., Thums, M., and Hume, I.D. 2004. Effects of diet change on carbon and nitrogen stable-isotope ratios in blood cells and plasma of the long-nosed bandicoot (*Perameles nasuta*). *Aust. J. Zool.* **52**: 635–647. doi:10.1071/ZO04029.
- Kurle, C.M., and Worthy, G.A.J. 2002. Stable nitrogen and carbon isotope ratios in multiple tissues of northern fur seal *Callorhinus ursinus*: implications for dietary and migratory reconstructions. *Mar. Ecol. Prog. Ser.* **236**: 289–300.
- Lowry, L.F. 1993. Foods and feeding ecology. In The bowhead whale. Edited by J.J. Burns, J.J. Montague, and C.J. Cowles. Spec. Publ. No. 2, Society of Marine Mammologists, Allen Press, Lawrence, Kans. pp. 201–238.
- Lowry, L.F., Frost, K.J., and Burns, J.J. 1980. Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. *Can. J. Fish. Aquat. Sci.* **37**: 2254–2261.
- Lowry, L.F., Burns, J.J., and Nelson, R.R. 1987. Polar bear, *Ursus maritimus*, predation on belugas, *Delphinapterus leucas*, in the Bering and Chukchi seas. *Can. Field-Nat.* **101**: 141–146.
- Lunn, N.J., and Stirling, I. 1985. The significance of supplemental food to polar bears during the ice free period of Hudson Bay. *Can. J. Zool.* **63**: 2291–2297.
- Lønø, O. 1970. The polar bear (*Ursus maritimus* Phipps) in the Svalbard area. *Nor. Polarinst. Skr.* **149**: 1–115.
- Mauritzen, M., Derocher, A.E., and Wiig, Ø. 2001. Space-use strategies of female polar bears in a dynamic sea ice habitat. *Can. J. Zool.* **79**: 1704–1713. doi:10.1139/cjz-79-9-1704.
- Mauritzen, M., Derocher, A.E., Wiig, Ø., Belikov, S.E., Boltunov, A., Hansen, E., and Garner, G.W. 2002. Using satellite telemetry to define spatial population structure in polar bears in the Norwegian and western Russian Arctic. *J. Appl. Ecol.* **39**: 79–90. doi:10.1046/j.1365-2664.2002.00690.x.
- Miller, S., Proffitt, K., and Schliebe, S. 2004. Demography and behavior of polar bears feeding on marine mammal carcasses. OCS study, MMS 2004, U.S. Department of the Interior, Anchorage, Alaska.
- Moore, S.E., DeMaster, D.P., and Dayton, P.K. 2000. Cetacean habitat selection in the Alaskan Arctic during summer and autumn. *Arctic*, **53**: 432–447.
- Paetkau, D., Amstrup, S.C., Born, E.W., Calvert, W., Derocher, A.E., Garner, G.W., Messier, F., Stirling, I., Taylor, M.K., Wiig, Ø., and Strobeck, C. 1999. Genetic structure of the world's polar bear populations. *Mol. Ecol.* **8**: 1571–1584. doi:10.1046/j.1365-294x.1999.00733.x. PMID:10583821.
- Pauly, D., Trites, A.W., Capuli, E., and Christensen, V. 1998. Diet composition and trophic levels of marine mammals. *ICES J. Mar. Sci.* **55**: 467–481. doi:10.1006/jmsc.1997.0280.
- Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* **18**: 293–320. doi:10.1146/annurev.es.18.110187.001453.
- Phillips, D.L., and Gregg, J.W. 2001. Uncertainty in source partitioning using stable isotopes. *Oecologia (Berl.)*, **127**: 171–179. doi:10.1007/s004420000578.
- Pond, C.M., and Gilmour, I. 1997. Stable isotopes in adipose tissue fatty acids as indicators of diet in arctic foxes (*Alopex lagopus*). *Proc. Nutr. Soc.* **56**: 1067–1081. doi:10.1079/PNS19970111. PMID:9483672.
- Polischuk, S.C., Hobson, K.A., and Ramsay, M.A. 2001. Use of

- stable-carbon and -nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. *Can. J. Zool.* **79**: 499–511. doi:10.1139/cjz-79-3-499.
- Quakenbush, L.T. 1988. Spotted seal, *Phoca largha*. In Selected marine mammals of Alaska: species accounts with research and management recommendations. Edited by J.W. Lentfer. Marine Mammal Commission, Washington, D.C. pp. 195–235.
- Ramsay, M.A., Nelson, R.A., and Stirling, I. 1991. Seasonal changes in the ratio of serum urea to creatinine in feeding and fasting polar bears. *Can. J. Zool.* **78**: 848–852.
- Reeves, R.R. 2002. The origins and character of 'aboriginal subsistence' whaling: a global review. *Mammal Rev.* **32**: 71–106.
- Regehr, E.V., Amstrup, S.C., and Stirling, I. 2006. Polar bear population status in the southern Beaufort Sea. Open-File Rep. 2006-1337, US Geological Survey, Alaska Science Center, Anchorage.
- Robbins, C.T., Hilderbrand, G.V., and Farley, S.D. 2002. Incorporating concentration dependence in stable isotope mixing models: a response to Phillips and Koch (2002). *Oecologia (Berl.)*, **133**: 10–13. doi:10.1007/s00442-002-0978-5.
- Roth, J.D., and Hobson, K.A. 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction. *Can. J. Zool.* **78**: 848–852. doi:10.1139/cjz-78-5-848.
- Rugh, D.J., and Shelden, K.E.W. 1993. Polar bears, *Ursus maritimus*, feeding on beluga whales, *Delphinapterus leucas*. *Can. Field-Nat.* **107**: 235–237.
- Sakashaug, E., Bjørge, A., Gulliksen, B., Loeng, H., and Mehlum, F. 1994. Structure, and biomass distribution, and energetics of the pelagic ecosystem in the Barents Sea: a synopsis. *Polar Biol.* **14**: 405–411.
- SAS Institute Inc. 1990. SAS[®]. Version 8.0 [computer program]. SAS Institute Inc., Cary, N.C.
- Scribner, K.T., Garner, G.W., Amstrup, S.C., and Cronin, M.A. 1997. Population genetic studies of the polar bear (*Ursus maritimus*): a summary of available data and interpretation of results. In Molecular genetics of marine mammals. Edited by A.E. Dizon, S.J. Chivers, and W.F. Perrin. Spec. Publ. Soc. Mar. Mammal. No. 3. pp. 185–196.
- Sease, J.L., and Chapman, D.G. 1988. Pacific walrus, *Odobenus rosmarus divergens*. In Selected marine mammals of Alaska: species accounts with research and management recommendations. Edited by J.W. Lentfer. Marine Mammal Commission, Washington, D.C. pp. 195–235.
- Smith, T.G. 1980. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. *Can. J. Zool.* **58**: 2201–2209.
- Smith, T.G., and Sjare, B. 1990. Predation of belugas and narwhals by polar bears in nearshore areas of the Canadian High Arctic. *Arctic*, **43**: 99–102.
- 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**(Suppl.): 59–76.
- Stirling, I., and Archibald, W.R. 1977. Aspects of predation of seals by polar bears. *J. Fish. Res. Board Can.* **34**: 1126–1129.
- Stirling, I., and Derocher, A.E. 1993. Possible impacts of climatic warming on polar bears. *Arctic*, **46**: 240–245.
- Stirling, I., and Lunn, N.J. 1997. Environmental fluctuations in arctic marine ecosystems as reflected by variability in reproduction of polar bears and ringed seals. In Ecology of arctic environments. Edited by S.J. Woodin and M. Marquis. Blackwell Science Ltd., Oxford. pp. 167–181.
- Stirling, I., and McEwan, E.H. 1975. The calorific value of whole ringed seals (*Phoca hispida*) in relation to polar bear (*Ursus maritimus*) ecology and hunting behaviour. *Can. J. Zool.* **53**: 1021–1027. PMID:1167176.
- Stirling, I., and Øritsland, N.A. 1995. Relationships between estimates of ringed seal (*Phoca hispida*) and polar bear (*Ursus maritimus*) populations in the Canadian Arctic. *Can. J. Fish. Aquat. Sci.* **52**: 2594–2612.
- Stirling, I., Spencer, C., and Andriashek, D. 1989. Immobilization of polar bears (*Ursus maritimus*) with Telazol[®] in the Canadian Arctic. *J. Wildl. Dis.* **25**: 159–168. PMID:2716095.
- Suydam, R.S., George, J.C., O'Hara, T.M., and Sheffield, G. 2002. Subsistence harvest of bowhead whales by Alaskan Eskimos during 2002. North Slope Borough, Department of Wildlife Management, Barrow, Alaska.
- Suydam, R.S., George, J.C., O'Hara, T.M., Hanns, C., and Sheffield, G. 2003. Subsistence harvest of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos during 2003. North Slope Borough, Department of Wildlife Management, Barrow, Alaska.
- Tieszen, L.L., Boutton, T.W., Tesdahl, K.G., and Slade, N.L. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia (Berl.)*, **57**: 32–37. doi:10.1007/BF00379558.
- Varanasi, U., Stein, J.E., Tilbury, K.L., Meador, J.P., Sloan, C.A., Clark, R.C., and Chan, S.L. 1994. Chemical contaminants in gray whales (*Eschrichtius robustus*) stranded along the west-coast of North America. *Sci. Total Environ.* **145**: 29–53. doi:10.1016/0048-9697(94)90296-8. PMID:8016628.
- Voigt, C.C., Matt, F., Michener, R., and Kunz, T.H. 2003. Low turnover rates of carbon isotopes in tissues of two nectar-feeding bat species. *J. Exp. Biol.* **206**: 1419–1427. doi:10.1242/jeb.00274. PMID:12624176.
- Watts, P.D., and Hansen, S.E. 1987. Cyclic starvation as a reproductive strategy in the polar bear. *Symp. Zool. Soc. Lond.* No. 57. pp. 305–318.
- Wiig, Ø., Derocher, A.E., and Belikov, S.E. 1999. Ringed seal (*Phoca hispida*) breeding in the drifting pack ice of the Barents Sea. *Mar. Mamm. Sci.* **15**: 595–598. doi:10.1111/j.1748-7692.1999.tb00828.x.