

Spatial and temporal variation in the diets of polar bears across the Canadian Arctic: indicators of changes in prey populations and environment

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Polar bears (*Ursus maritimus*) are broadly distributed in the Arctic and, as such, have the potential to provide information about changes in ecosystem structure and functioning over broad scales in time and space. Yet, because they are so wide-ranging and difficult to observe, there are few quantitative data on polar bear diets or on the ecological (e.g. climate change) and demographic factors that influence prey selection. We used quantitative fatty acid signature analysis of polar bear adipose tissue to estimate their diets in the 1980s/90s across three major regions of the Canadian Arctic: Davis Strait ($n = 70$), western Hudson Bay ($n = 217$) and the Beaufort Sea ($n = 34$), using a database of the major prey species in each region ($n = 292$). Although polar bears consumed ringed and bearded seals throughout their range, diets differed greatly among regions. Ringed seals accounted for $\geq 98\%$ of diet in the Beaufort Sea. In western Hudson Bay, ringed seals accounted for about 80% of intake in the early 1990s, indicating the importance of foraging in ice-covered habitat. However, ringed seal consumption declined throughout the 1990s concurrent with progressively earlier ice breakup, while the proportions of bearded and harbour seals increased, suggesting reduced reliance on ice. Throughout Davis Strait, harp seals comprised 50% of bears' diets, consistent with the increase in the harp seal population in this region. Off southern Labrador near the whelping patch, harp seals accounted for 90% of diets. Hooded seals made up the highest proportion of bear diets in northern Davis Strait, near their major northern whelping patch. Our results demonstrate that polar bears have a high

degree of plasticity in response to changing environments and prey populations, which suggests that they may be excellent indicators of ecosystem changes.

Apex predators occupy a special niche in their ecosystems, playing an important role in ecosystem structure and functioning, but also being affected by changes at lower trophic levels (e.g. Katona & Whitehead 1988, Estes 1995, Bowen 1997, Terborgh *et al.* 1999). Because top predators are often large, long-lived and geographically wide-ranging, characteristics of their populations can potentially serve to integrate the cumulative effects of ecosystem change over a range of spatial and temporal scales. In the Arctic, polar bears represent the highest trophic level and their circumpolar distribution is determined by the distribution of their preferred habitat, the annual ice over the continental shelf. They depend on ice for hunting and feeding on the seals that use ice as a platform for parturition and lactation, and for hauling out to rest and moult. Those bears that live on the pack ice all year round, such as in the Beaufort Sea, move north with the receding floe edge in summer and south again in winter (Amstrup *et al.* 2000). The southernmost populations live year-round in the Hudson and James bays, Canada, where ice is completely absent for at least 4 months during summer and autumn each year, and all bears are forced ashore to fast until freeze-up, while pregnant females fast for 8 months (Stirling *et al.* 1977, Ramsay & Stirling 1988). Thus, the presence of sea-ice is critical to polar bears and changes in its distribution and duration will have a profound impact on their foraging patterns and population ecology (Stirling & Derocher 1993, Stirling *et al.* 1999).

Although it is commonly held that polar bears feed predominantly on ringed seals (*Phoca hispida*) throughout their range (Stirling & Archibald 1977, Smith 1980), bears also occur in areas where ringed seals are less common and where populations of other potential prey species have increased over recent decades. These other prey species could have a significant influence on the distribution, movements, reproductive success and dynamics of polar bear populations. Thus, as very widely distributed top predators in the Arctic, long-term monitoring of the foraging ecology and diets of polar bears may provide insight into temporal and spatial changes in the Arctic ecosystem at local, regional and circumpolar scales.

Despite their potential importance, polar bear diets are difficult to study and estimate quantitatively because of the extreme spatial heterogeneity and dramatic seasonal variation in prey distribution in the Arctic and the difficulty in directly observing predation. In Canada, there are 14 designated subpopulations of polar bears that appear to be relatively discrete based on movements and microsatellite analyses (Paetkau *et al.* 1999, Taylor & Lee

1995), however some individuals may travel distances of up to 6000 km per year (Amstrup *et al.* 2000). To date, our understanding of the foraging ecology of polar bears has come predominantly from carcasses of seals killed by bears and direct observations, primarily from one field site in the eastern high Arctic. Most of these studies have been conducted between late March and early July prior to ice breakup, yet bears' hunting behaviour on the coastal landfast ice and adjacent floes may not be representative of the entire year. Thus, our understanding of polar bear diets is incomplete and new approaches are needed.

Quantitative fatty acid signature analysis (QFASA; Iverson *et al.* 2004) is one such approach. This method is based upon the observation that the characteristic fatty acid (FA) patterns of prey species are predictably reflected in the adipose fat reserves of monogastric predators. Polar bears should be ideally suited to the application of QFASA, given the generally high fat content of their diets (Stirling, 1974, Smith, 1980) – which limits biosynthesis of FAs – and because their large depots of body fat are accumulated over months, providing an integrated view of the diet. Polar bears also are thought to eat relatively few prey species (about two to eight species), depending on their geographical region (Stirling & Øritsland 1995), which simplifies diet estimation. We used QFASA to ask how well polar bear diets reflect relative abundance or changes in prey populations across the Canadian Arctic and thus whether bears might be used as indicators of ecosystem change.

SAMPLE COLLECTION

We obtained 321 adipose tissue samples from 295 bears (some bears were sampled in more than one year) across three regions of the Canadian Arctic, representing four subpopulations (Fig. 7.1). Subcutaneous adipose tissue samples from muscle to skin were obtained from the rump either from biopsies (6-mm biopsy punch) from anaesthetized bears – in association with tagging and monitoring programmes of the Canadian Wildlife Service – or from bears harvested by Inuit hunters. FA composition of subcutaneous adipose tissue does not differ significantly among body locations within individual bears (Thiemann *et al.* in press).

Given that polar bears consume primarily the blubber of seals and that the blubber will represent the majority of FAs stored in a seal even if the entire carcass was consumed, we assumed that the blubber of seals was representative of prey FAs. We obtained full-depth blubber samples by live biopsy or from subsistence harvests from 292 individuals (across age classes) of six species: bearded (*Erignathus barbatus*), harbour (*Phoca*

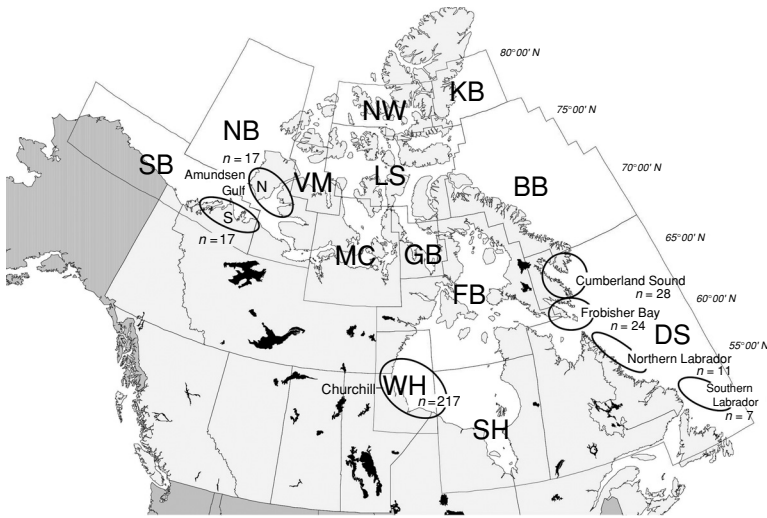


Fig. 7.1 Currently designated Canadian polar bear subpopulations. Abbreviations are: BB, Baffin Bay; DS, Davis Strait; FB, Foxe Basin; GB, Gulf of Boothia; KB, Kane Basin; LS, Lancaster Sound; MC, M'Clintock Channel; NB, Northern Beaufort Sea; NW, Norwegian Bay; SB, Southern Beaufort Sea; SH, Southern Hudson Bay; VM, Viscount Melville Sound; WH, Western Hudson Bay. Circles indicate the areas and associated sample sizes of polar bears sampled in the present study: NB, SB, WH and four regions within the DS population. Most (95%) of the samples were taken throughout the 1990s, although a few were available from the early 1970s and 1980s. In NB, SB and DS, bears were mostly sampled on the ice in late winter and spring. In WH, most bears were sampled on land after ice breakup.

vitulina), harp (*Phoca groenlandica*), hooded (*Cystophora cristata*) and ringed seals and walrus (*Odobenus rosmarus*). Bearded and ringed seals were sampled from the same regions as the bears. Given their regional distribution, walrus, and harp and hooded seals were sampled from the Davis Strait (DS) designation (Fig. 7.1) and harbour seals from the western Hudson Bay (WH). Although polar bears are known to occasionally feed on belugas (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*), as well as other prey (e.g. Smith & Sjare 1990, Derocher *et al.* 1993, 2000), we felt we had obtained the species most likely to comprise the majority of diets of the bears from the populations included in this study.

VARIATION IN FA COMPOSITION OF POLAR BEARS AND PREY

Lipid was quantitatively extracted from samples according to Iverson *et al.* (2001a) and FA composition was analysed according to Budge *et al.* (2002)

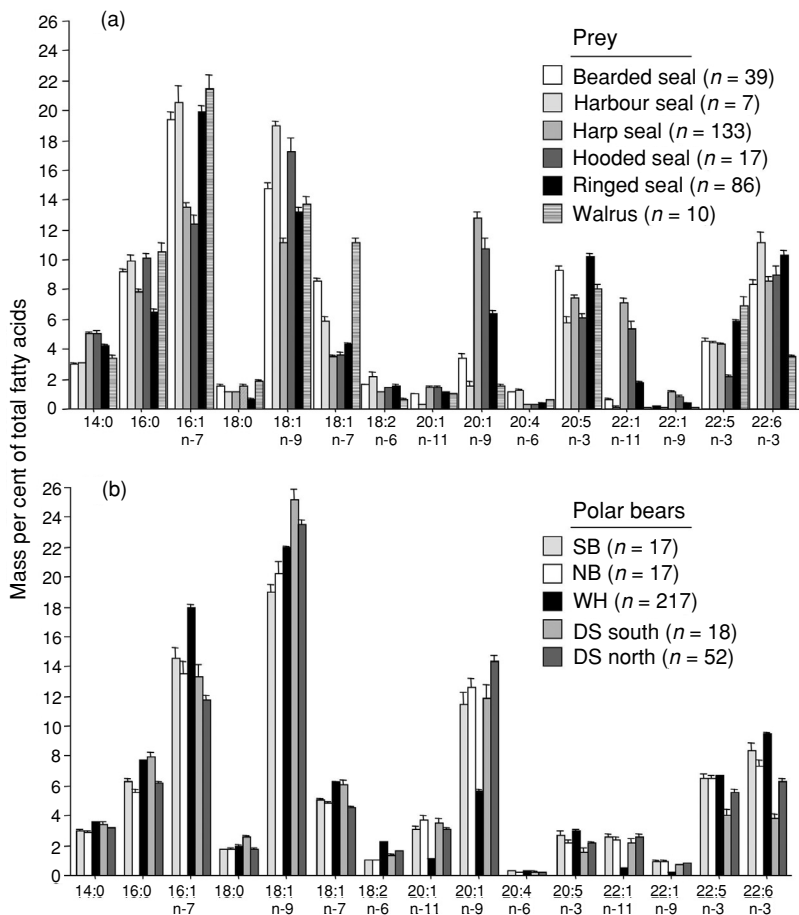


Fig. 7.2 Selected FAs (mean + sem; 15 of the 67 FAs identified and quantified, representing 87% to 88% of all FAs in both seals and polar bears) that were most abundant and/or exhibited the greatest average variance across all groups: (a) in prey species averaged across all regions of the Canadian Arctic sampled and (b) in polar bears within the four sampled subpopulations. Given the large range in latitude of bears sampled in the DS population, these were separated into northern and southern areas (for abbreviations and areas see Fig. 7.1).

and Iverson *et al.* (2002). All seals and bears contained the same major FAs, however, the FA composition varied markedly among prey species and among bears across locations (Fig. 7.2a and b). Many of the key dietary FAs such as 20:1n-9, 20:5n-3, 22:1n-11 and 22:6n-3, tended to characterize both prey and bears in different regions, but means of individual FAs are a limited way to view data. Discriminant function analyses test predicted group

membership and classification success, but also serve to illustrate spatial relationships between groups. Prey were generally accurately identified to species by their FA signature, but there was also indication of variation within species across the Arctic (Fig. 7.3a). Bearded and ringed seals were each classified to species with 93% to 97% accuracy, and to geographical location within species with 75% to 85% accuracy, indicating some regional variation in food webs and diets of those species. Harp and hooded seals were each classified with about 80% accuracy, but exhibited the greatest overlap; when misclassified, it was generally harp seal wrongly classified as hooded seal and vice versa. Walrus differed most from other species and were classified with 100% success. Hierarchical cluster analyses (in which a single average for each group is tested therefore allowing a larger subset of FAs to be used) supported these results, with species being the major grouping factor – within which there was regional variation. Together these results are consistent with general differences in the diets of these prey species (e.g. Bowen & Siniff 1999).

Polar bears exhibited marked variation in FA signatures across regions of the Arctic (Fig. 7.2b), indicating regional differences in diet. Using discriminant function analysis, bears were 100% correctly classified to their subpopulations (Fig. 7.3b). Within DS, there was clear indication of differences in diets between northern and southern groups with 100% and 94.4% correct classification, respectively. Nevertheless, some overlap was apparent.

QFASA MODELLING AND POLAR BEAR DIETS

We used the QFASA model developed by Iverson *et al.* (2004) to perform simulation studies of diets and to estimate diet composition of polar bears (Box 7.1). Simulation studies were first performed to confirm the reliability with which prey species could be differentiated in the model estimates. All simulations indicated that prey species were well estimated in specified diets, providing confidence that these prey species can be reasonably estimated in the diets of sampled bears. For the purposes of the current study, we did not attempt to separate age classes of seal prey in simulations or diets, as variation was far greater between than within species (e.g. Fig. 7.3a, Box 7.1).

The diets of polar bears were estimated using QFASA as modified for polar bears (Box 7.2). Because of the large spatial scale over which we sampled bears (North Atlantic to Beaufort Sea), we used location-specific prey assemblages and corresponding FA signatures. Harbour seals and walrus

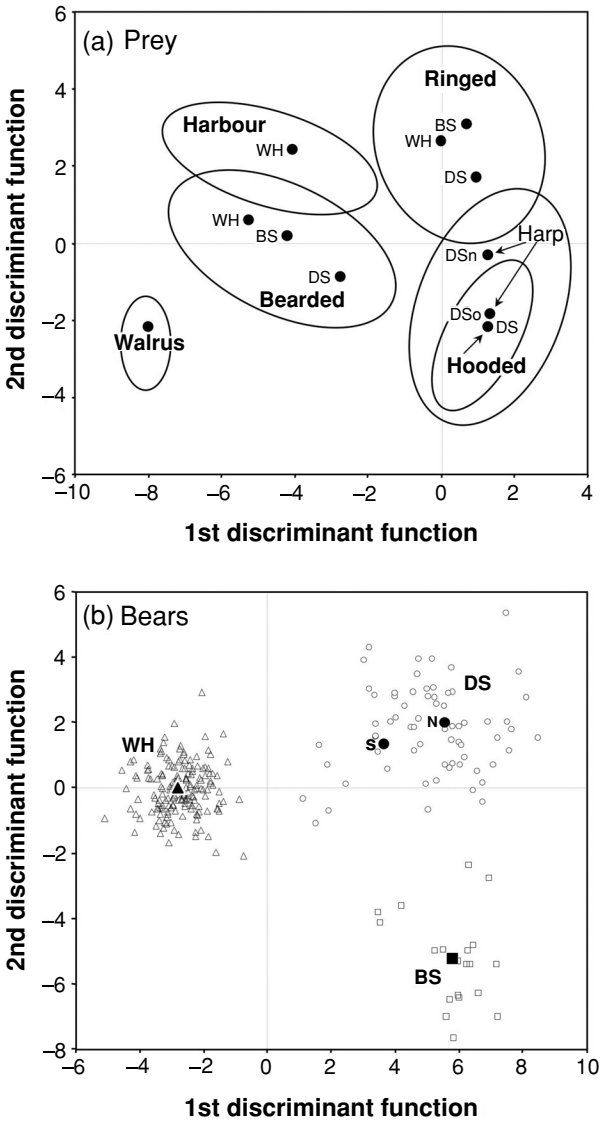


Fig. 7.3 Results of discriminant function analyses of seals and polar bears across the Canadian Arctic. Due to small sample sizes for some prey species (e.g. $n = 7$) and bears in some locations (e.g. $n = 17$, see Fig. 7.2), we used a reduced set of FAs (one minus size of the smallest group, respectively) for discriminant analyses, to offer some assurance that covariance matrices were homogeneous (Stevens 1986). Here we used FAs that were most abundant and/or exhibited the greatest average variance across all groups, and analyses were performed according to Iverson *et al.* (2002). (a) Plot of the group centroids (within-group

do not generally occur in the areas of bears sampled in the northern and southern Beaufort (NB and SB, Fig. 7.1). Thus these bears were modelled only on ringed and bearded seals ($n = 24$ prey) collected in the Beaufort Sea. Hooded seals do not occur in WH and harp seals or walrus are available only occasionally. Nevertheless, we modelled WH bears on ringed, bearded and harbour seals (obtained in WH), and also included harp seals and walrus (obtained in DS, Baffin Bay (BB) and Foxe Basin (FB), Fig. 7.1; $n = 120$ prey). We were not able to obtain samples of harbour seals in DS given their rarity there, but all other species are potentially available to bears in this area. Thus, DS bears were modelled using ringed, bearded, harp and hooded seals and walrus collected in the DS area ($50^{\circ} 00'$ to $70^{\circ} 0'$ N, Fig. 7.1; $n = 231$ prey).

Consistent with differences in FA signatures of polar bears (Figs 7.2b and 7.3b), their estimated diets differed dramatically across their geographic range (Fig. 7.6). Although ringed and bearded seals occurred in bear diets throughout the Canadian Arctic, their relative importance differed greatly. In both NB and SB, ringed seals comprised about 95% of the FA signatures of polar bear adipose tissue, with the remainder being made up by bearded seals (Fig 7.6a). However, on average in WH, ringed seal consumption accounted for only 56% of FA signatures, followed by about 38% bearded and 5% harbour seal; trace levels (<1%) of harp seal also appeared. In the DS subpopulation, ringed and bearded seals accounted for 18% and 26% of signatures, respectively, whereas harp seals (49%) dominated; some hooded seals (12%) were also present. While both harp and hooded seals were reasonably well differentiated in simulations, there was evidence for some degree of overlap in signatures (Box 7.1; Fig. 7.3a). Thus, the precise proportions estimated for these two species are somewhat less certain. Walrus appeared at about 1% of diets in DS overall (Fig. 7.6a).

← Fig. 7.3 (cont.) mean for each discriminant function) for the first and second discriminant functions for prey species by region. Ellipses represent 95% of the data points for each species. The first two functions accounted for 86.9% of the variance among the 11 groups tested ($n = 292$; Wilk's $\lambda < 0.001$). Species overall were separated with 86.6% accuracy. For harp seals, DS_n and DS_o represent individuals sampled in DS nearshore and DS offshore, respectively. (b) Plot of the discriminant scores for each individual polar bear ($n = 257$, removing repeat-sampled bears and cubs), as well as the group centroids, for the first and second discriminant functions. NB and SB bears were combined as BS (Beaufort Sea), due to close proximity of sampling. The first two functions accounted for 95.0% of the variance (Wilk's $\lambda < 0.001$) and individuals were grouped to major region (Fig. 7.1) with 99.6% accuracy overall; the only misclassifications were between northern and southern DS.

Box 7.1 FA signatures, QFASA and diet simulations

FAs are the main constituent of most lipids. During digestion, FAs are released from ingested lipid molecules (e.g. triacylglycerols), but unlike other nutrients – such as proteins – which are readily broken down, FAs are generally not degraded. The FAs of carbon chain-length 14 or greater pass into the circulation intact and the fraction not required for immediate metabolic needs is taken up and deposited in adipose tissue in a predictable way. Since a relatively limited number of FAs can be biosynthesized by animals, it is possible to distinguish dietary versus non-dietary components. Numerous studies have demonstrated qualitatively that specific FAs and patterns of FAs are passed from prey to predator both near the bottom and top of terrestrial and marine food webs (reviewed in Iverson *et al.* (2004)). QFASA is based on the notion that most prey have characteristic FA signatures (i.e. the quantitative distribution of all FAs measured; e.g. Budge *et al.* 2002, Iverson *et al.* 2002), that these signatures are deposited in predator adipose tissue in a predictable way and that by comparing FA signatures of all potential prey to those of predator adipose tissue using a statistical computer model (Iverson *et al.* 2004), one can determine what was eaten. Briefly, QFASA asks what mix of prey species' FA signatures comes closest to matching that of the predator.

Following this approach, the first requirement for estimating predator diets is a representative database of potential prey species and an understanding of whether those species can be reliably distinguished from one another by their FA signature. While various univariate and multivariate statistical techniques can be used for such purposes, a powerful means with which to test the ability of the QFASA model to estimate diet – based solely on differentiating and quantifying prey species by their FA signatures – is to perform simulation studies (Iverson *et al.* 2004). The basic procedures are as follows: a diet composition of a polar bear was specified (e.g. 80% ringed seal, 20% bearded seal). For each prey species, the individual samples were split into two equal sets: a simulation set and a modelling set. A 'pseudo bear' was constructed by sampling from the simulation set in the proportions specified by the simulated diet. The 'diet' of this pseudo bear was then modelled using the modelling

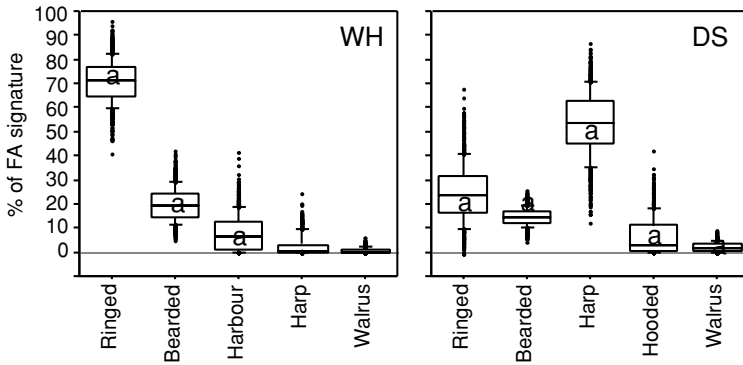


Fig. 7.4

set of those prey species plus all other prey in the region's database. This creation of the pseudo bear and subsequent modelling was then repeated 1000 times and gave an indication of mean reliability of estimates and noise around those estimates.

Figure 7.4 shows the results of the simulation studies for WH and DS presented as box plots, showing the 25th, median, and 75th percentiles of the 1000 diet estimates as horizontal bars and with dots representing outliers. The diet composition specified is represented in plots as 'a' and was designated as follows. For WH, composition was designated as 75% ringed seal, 20% bearded seal and 5% harbour seal; for DS, it was 20% ringed seal, 20% bearded seal, 50% harp seal, 8% hooded seal and 2% walrus. The simulations performed for each region demonstrated the reliability with which we could differentiate prey species of polar bears in the QFASA model. In WH, ringed, bearded and harbour seals were well estimated in diets, with only trace amounts of noise from the appearance of harp seals or walrus. When harp seal and walrus were removed from the simulations, results were similar except that the proportions of all prey items were precisely predicted as specified. In DS, species were again well estimated with some overlap between harp and hooded seals. Ringed seals were only slightly overestimated and bearded seals only slightly underestimated. Results for the Beaufort Sea (not shown) also showed precise estimates of specified diets.

Box 7.2 The QFASA model and calibration as applied to polar bears

Although dietary FAs directly influence predator lipid stores, some metabolism of FAs does occur within the predator, such that the composition of predator tissue will not exactly match that of their prey. Thus, an understanding of and accounting for, the process by which ingested FAs are metabolized and deposited in tissues of the predator is fundamental to the use of FAs in food-web studies. An integral part of the QFASA model is the use of calibration coefficients to account for predator lipid metabolism by weighting individual FAs (Iverson *et al.* 2004). Previous coefficients have been calculated for blubber of juvenile and adult phocid¹ seals fed fish diets and for suckling phocid pups consuming high-fat milk diets. Since the blubber of pinnipeds is more structured than that of simple adipose tissue (Iverson 2002), we felt it important to develop a more appropriate model species for polar bear adipose tissue. We used data obtained from feeding and fattening mink (*Mustela vison*) kits ($n = 18$) on a long-term homogenous diet supplemented with marine oil.

Figure 7.5 shows the calibration coefficients for mink (mean \pm SEM of the 10% trimmed means calculated within each individual; note, in most cases the SE is too small to see) estimated for all 67 FAs quantified (calculated from Layton (1998) and Iverson *et al.* (2004)). The 15 most abundant FAs found in both polar bears and seals are labelled. The 1:1 line is presented which denotes the deviation of a given FA in a predator from that consumed in its diet. The calibration coefficients calculated for mink were generally similar to those for phocid pups on high-fat diets – although with some exceptions – and were consistent with our current understanding of how specific FAs are metabolized (Cooper *et al.* 2005).

The model proceeds by applying the calibration coefficients to the FAs of the predator's stores. It then takes an average, or series of averages, of each prey FA signature and asks what mix of prey signatures comes closest to matching a given calibrated predator. Finally, a statistical distance is calculated between the real predator and the model's estimate of that predator and chooses the weighting that minimizes the statistical distance to represent the best estimate of diet (see Iverson *et al.* (2004) for details).

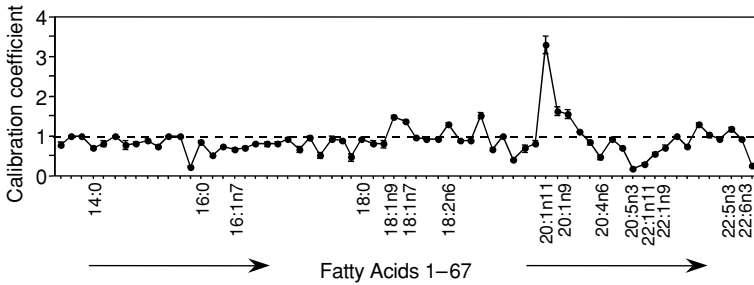


Fig. 7.5

We modelled bears using the two subsets of FAs outlined in Iverson *et al.* (2004) ('dietary', which includes only those 33 FAs that arise solely or mostly from dietary origin; and 'extended dietary', which includes an additional 8 FAs that are abundant in diet but are also biosynthesized), and using several sets of calibration coefficients (mink, phocid pup and no calibration). The results of modelling scenarios using the two FA subsets and the different calibration coefficients were generally comparable within major geographic region, although this depended somewhat on the complexity of the prey database. In the Beaufort Sea (BS), diet estimates of bears were nearly identical using either dietary or extended FA subsets and using mink, phocid pup or even no calibration; probably because the two prey species available differed substantially in their FA signatures. However, in both WH and DS, modelling with the dietary FA subset and mink calibration provided the most consistent results: we evaluated this by modelling bears in each area with additional prey added to the model from other areas that we knew could not occur in the diets due to their geographic range. We found little, if any, false positives when using dietary FAs and mink calibration. Given that there were a-priori reasons to suggest that mink calibration would be most appropriate for bears, we report only these results.

¹ Inclusive of all true seals and exclusive of sea lions, fur seals and walrus.

The above diet estimates represent the total mass contribution of each prey species' blubber FAs to polar bear diets. However, these species differ greatly in body size. Although by no means definitive, we used one simple approach to illustrate the relative difference in diet estimates if one accounts for these differences in species body mass and thus total blubber

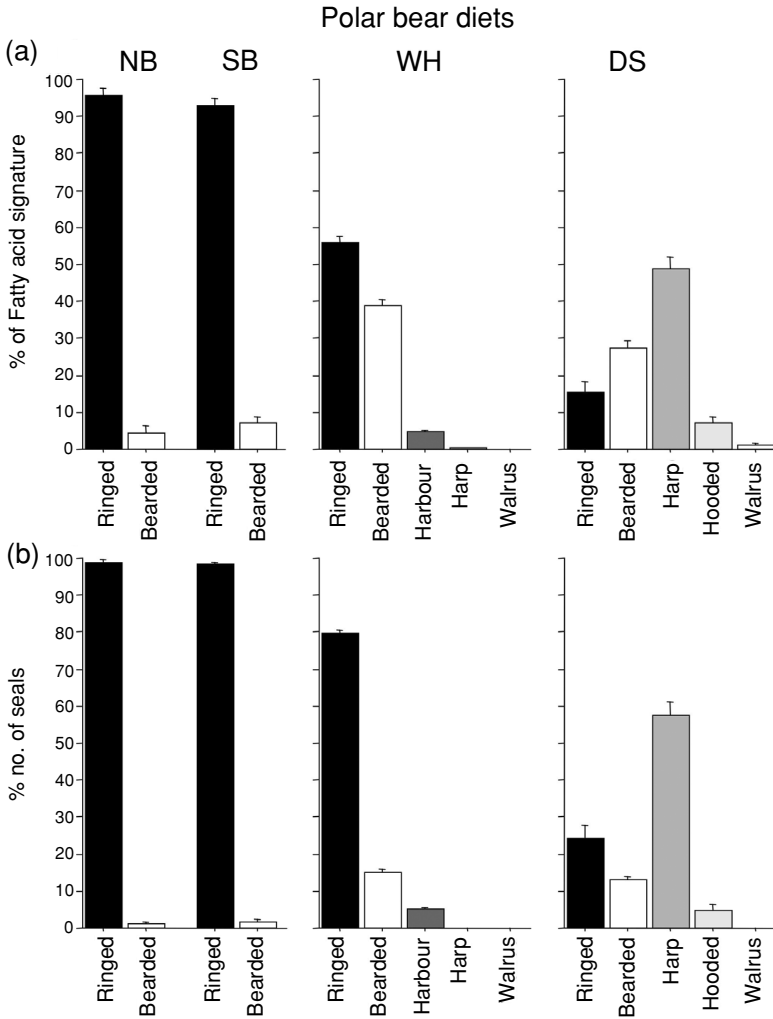


Fig. 7.6 QFASA model estimates (mean + SEM) of polar bear diets across the three major geographical regions and four subpopulations. (a) Data are presented as the QFASA model output, or the proportional contribution of prey species to polar bear adipose tissue FA signatures. (b) Data are presented as the approximate percentage number of seals that would be consumed to account for these signatures given the large size differences among prey species. For these estimations, we made the coarse assumption that the entire carcass's blubber layer was consumed, that seals contained similar percentages of blubber and, finally, that both juveniles and adults of each species scaled similarly by body size. We used the following adult body mass values for scaling: ringed (65 kg), bearded (300 kg), harbour (87 kg), harp (110 kg) and hooded seal (250 kg); walrus (1040 kg); ringed seals were used as the divisor.

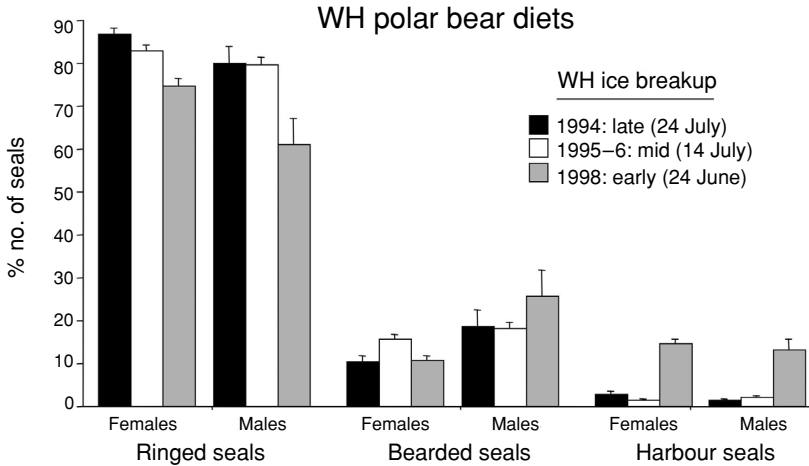


Fig. 7.7 QFASA estimates of female ($n = 86$) and male ($n = 99$) polar bear diets (mean percentage of relative number of seals \pm SEM; see Fig. 7.4) in WH during a 5-year period in relation to timing of ice breakup (Stirling *et al.* 1999) in those years. Only bears >1.5 years of age and sampled in summer after coming ashore with the ice melt were included. Diets of females and males differed in all components ($p \leq 0.01$), diets decreased in levels of ringed seals and increased in harbour seals in both females and males ($p \leq 0.01$), and diets were variable in levels of bearded seals ($P = 0.236$; two-way ANOVA). Results were the same when expressed as a percentage of FA signature or as converted to a proxy of relative number of seals (shown).

available (Fig. 7.6b). In this scenario, diets translated into somewhat different percentages of the relative number of seals taken by bears. Ringed seals represented the dominant seal taken in the Beaufort Sea (almost 100%) and WH (80%). In contrast, harp seals constituted 60% of seals taken in DS. Walrus fell to non-detectable levels in both WH and DS overall (Fig. 7.6b).

Changes in diet were also associated with environmental variation. Polar bears in WH were sampled in 1994, 1995, 1996 and 1998 – years of progressively earlier ice breakup (Stirling *et al.* 1999). Diets in the region differed significantly between female and male bears in all years, but also changed in relation to annual timing of ice breakup (Fig. 7.7). Females consumed more ringed seals and fewer bearded seals than did males. However, between the year of latest ice breakup (1994) and that of the earliest ice breakup (1 month earlier, 1998), ringed seals declined in the diets of both sexes, with a corresponding increase in harbour seals and variably increasing numbers of bearded seals (Fig. 7.7).

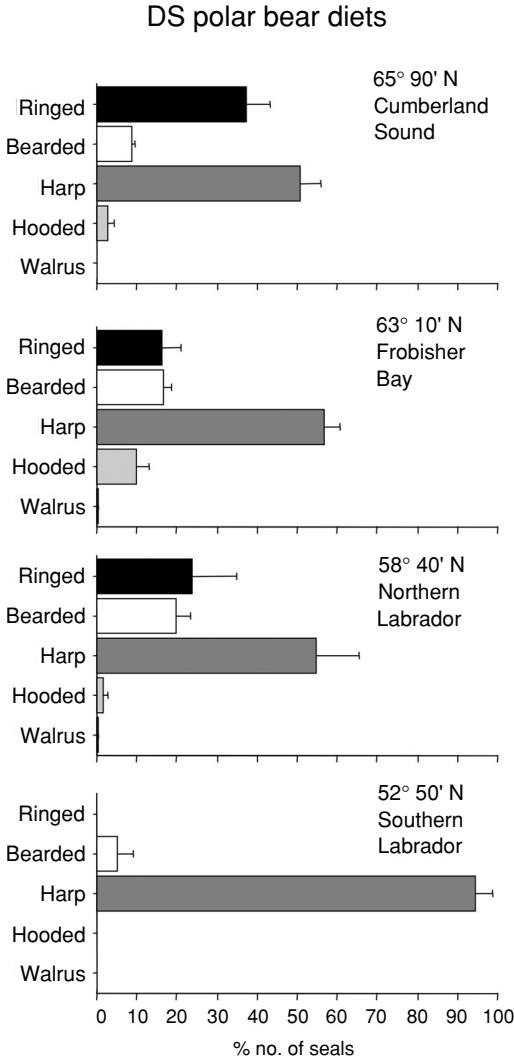


Fig. 7.8 QFASA estimates of polar bear diets (mean percentage of the relative number of seals + SEM; see Fig. 7.6) across the wide range of latitudes of bears sampled within the DS population (*see* Fig. 7.1). Bears in southern Labrador consumed more harp seals and fewer (none) ringed seals than in all other areas ($p < 0.01$), and consumed fewer bearded seals than in all areas except Cumberland Sound ($p < 0.01$). The greatest numbers of hooded seals were consumed by bears sampled near Frobisher Bay ($p < 0.05$). Walrus consumption did not differ with area (ANOVA with Fisher's PLSD *post-hoc* tests).

Polar bear diets also varied spatially within a subpopulation as a function of latitude. Diets differed notably in bears from the southern- and northernmost areas of the DS subpopulation (Fig. 7.8). Harp seals accounted for 90% of seals consumed by the seven bears sampled in southern Labrador, whereas they comprised a lower and relatively constant proportion of the seals consumed further north. In contrast, ringed seals were absent from diets of southern Labrador bears but gradually increased in diets to the north, as did bearded seals. Hooded seals were consumed most in the areas near Frobisher Bay. Walrus were estimated as appearing in diets of only eight individuals from northern areas of DS: five males and three females. In three bears, walrus were estimated to contribute a large amount to FA signatures (11% to 24%), although this translated into only 1% to 5% of the seals consumed.

POLAR BEARS AS INDICATORS OF ARCTIC ECOSYSTEMS AT REGIONAL AND CONTINENTAL SCALES

The results of our study provide new insight into the foraging ecology of polar bears across their Canadian range. Although FAs have been used previously to make inferences about changes in lower trophic levels in an ecosystem (Iverson *et al.* 1997, 2001b), this is the first time FAs have been used to estimate quantitatively the diets of a top predator in relation to spatial and temporal changes in prey availability.

Previous studies, based on direct observation, have concluded that ringed seals are the dominant prey of polar bears in the Arctic, followed by bearded seals (e.g. Stirling 2002). However, climate and access have limited most studies of polar bear foraging to late winter and early spring, and to areas of landfast sea-ice and immediately adjacent pack-ice where ringed seals are most abundant, thus potentially biasing our concept of their importance in the diet. Nevertheless, ringed seals clearly remained an important component of polar bear diets in this study (Fig. 7.6). However, their dominance (and even presence) in diets across spatial and temporal scales differed dramatically. In the bears sampled in NB and SB in the early 1990s, ringed seals were consumed almost exclusively, consistent with their distribution and abundance relative to bearded seals in those areas (e.g. Stirling 2002). Similarly, ringed seals were the dominant seal consumed in WH, but this varied substantially by individual, sex and year (e.g. Fig. 7.7). Male bears fed more on bearded seals than did females, which is consistent with expectations based on their larger body size and more frequent (albeit limited) observations of male bears seen over bearded seal kills than females

(Stirling & Derocher 1990). This has interesting implications for evaluating male foraging and consumption. A bearded seal is over four times heavier than a ringed seal, and thus a bear would only need to catch a single bearded seal to equal the blubber intake of four to five ringed seals. Future determination of age classes of seals taken will also influence these conclusions. Despite potential sex differences in foraging tactics, both sexes responded to environmental variability in similar ways and thus both served as indicators of short-term ecosystem change.

During the 1990s in WH, the trend towards progressively earlier sea-ice breakup dates was accompanied by significant decreases in ringed seals in polar bear diets. Through the same period, Holst *et al.* (1999) and Stirling (2004) documented low apparent survival of ringed seal pups in 1998–2000. It is not clear whether the increase in the proportion of bearded and harbour seals in the diet of WH bears through the 1990s reflects a decline in the availability of ringed seals, an increase in the population size and availability of bearded and harbour seals, or both. However, all species are mainly only available to bears on the ice so these changes in diet, especially reduction in ringed seals, complement evidence that during the same period bears came ashore earlier and in progressively poorer condition, with a decline in both physical and reproductive characteristics (Stirling *et al.* 1999).

Besides short-term temporal changes, diet composition of apex predators can characterize, and signal a shift in, the abundance of lower trophic levels. In WH, bear diets reflected their prey field as an assemblage dominated by ringed and bearded seals, with increasing dependence on both harbour and bearded seals, coincident with climate warming as predicted by Stirling and Derocher (1993). Little or no harp seal and walrus occurred in diets, consistent with their known geographic distributions, further supporting the notion that the FAs of polar bears reflect the prey available. In DS, bear diets reflected a longer-term trend in prey abundances. Although it was previously known, mostly from chance encounters, that polar bears hunted harp seals, we have for the first time shown that harp seals are the dominant prey in this region, along with some intake of hooded seals. This coincides with the large and well-documented increases that have occurred in these seal populations since the early 1970s (NOAA 1999, DFO 2000) and with apparently increasing polar bear numbers observed in this area (I. Stirling, unpublished data, 2005). Harp seals were most abundant in the diets of bears in southern Labrador, which is closest to the harp seal whelping patch, while hooded seals were most abundant in diets of bears near Frobisher Bay ($63^{\circ} 10' \text{ N}$), which is closest to the northern hooded seal whelping patch (62° to 64° N). These results are consistent with both

known geographic distributions and abundances of prey species, but also with large and longer-term changes in population size. While we have focused the present study on the major prey of polar bears, future studies should seek to include more minor, and potentially increasing, prey species.

Overall, we conclude that polar bear diets accurately reflect changes in prey populations and thus are useful indicators of ecosystem change. Changes occurring in polar bear diets in WH were consistent with relatively short-term indications of temporal changes. In contrast, diets of bears in DS accurately reflected both long-term trends in species abundance as well as geographic variation in relation to the availability of different species. Taken across the entire Canadian Arctic, from NB and SB to WH and DS, the differences in diets of polar bears reflected both the distribution and abundance of species across a continental scale. Long-term changes in climate and ecosystems are occurring. Perhaps, nowhere is this more apparent than in the Arctic (e.g. Tynan & DeMaster 1997). We conclude that long-term monitoring of the diets of polar bears, using the methods we have set forth, along with data on other aspects of their population dynamics, will provide invaluable information relevant to understanding changes in Arctic ecosystems at both regional and continental scales.

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