The numbers of ringed seals (*Phoca hispida*) in Baffin Bay and associated waters

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ABSTRACT

The size of the population of ringed seals (*Phoca hispida*) inhabiting Baffin Bay and associated waters was estimated by two methods. An approximate model of the energetics of the polar bear (*Ursus maritimus*) estimated an energetic need of about 16,000 MJ/bear per year. Modelled estimates of the energetic yield of a ringed seal population showed that a stable standing population of 140-170 ringed seals per bear would be needed to provide that much energy, assuming that all mortalities were due to polar bear predation. This result was sensitive to assumptions about the Field Metabolic Rate (FMR) of the bears and the energetic yield of individual ringed seals, but less sensitive to assumptions about relative incidence of predation on different age classes of seal or the age structure of the polar bear population. Estimated sizes of polar bear populations in Baffin Bay and associated waters (total about 4,025), and of the standing population needed to support an estimated hunter kill of 100,000 yielded a population estimate of, very roughly, 1.2 million ringed seals. Estimates of ice areas and of the density of hauled out seals from aerial surveys were used to generate another approximate figure for the ringed seal population, which was about the same. The density of seals in the pack-ice area of Baffin Bay, which is imperfectly known, has a large influence on the latter estimate.

INTRODUCTION

Estimating the true size of populations of the ringed seal (*Phoca hispida*), like those of other marine mammals, is difficult. They spend an unknown proportion of their time under water, or under the ice, they inhabit wide, remote areas that are difficult to survey, and they are difficult to capture and mark. Among the methods proposed or used are ship surveys (e.g. McLaren 1961), aerial surveys, visual, photographic, or infra-red (e.g. Burns and Harbo 1972, Smith 1975, Stirling *et al.* 1982, Kingsley *et al.* 1985, Born *et al.* this volume) of seals or seal holes, and searches of the ice surface for holes or lairs using dogs (Smith and Stirling 1978, Hammill and Smith 1990). Most of these methods are subject to uncertainties as to what fraction of the population is available to be counted (Finley 1979, Smith and Hammill 1981), or the relation between an index, such as seal holes or lairs, and the population size, or they are simply limited in the area that can be covered. Although the ringed seal is an important species in the Arctic food web, these problems of population estimation have not been entirely solved. However, local study of the biology of ringed seals has allowed estimates to be made of its life history and population dynamics (McLaren 1958, Smith 1973, 1987).

The polar bear (*Ursus maritimus*) has been intensively studied, and relatively good information exists as to its population size, dynamics, and structure, and its movements, diet and behaviour. It is thought to feed almost entirely on ringed seals over most of its range. It should therefore be possible, through a predator-prey model, to relate predation on ringed seals to the estimated energetic needs of a polar bear population (Kingsley 1990a, Stirling and Øritsland 1995). With the addition of a population model for ringed seals, a means of calculating the standing population of ringed seals necessary to maintain a polar bear population can be obtained.

This article describes a model of the size and structure of a hypothetical polar bear population and from this calculates how much energy the average bear needs. By modelling the structure of a ringed seal population, it is possible to calculate how much energy predators can gain from a standing population of a given size. So by equating the two, we can estimate an approximate ratio of the predator and prey populations, and so from the predator estimate the size of its prey base. The estimated size of polar bear populations in Baffin Bay and the associated waters, Kane Basin, Jones Sound, eastern Lancaster Sound, and Ungava Bay and eastern Hudson Strait (Fig.1), was then applied to this model to estimate the ringed seal population in that area. Furthermore, data from aerial surveys of ringed seals in the Baffin Bay and adjacent waters were used to derive an alternative estimate for comparison.

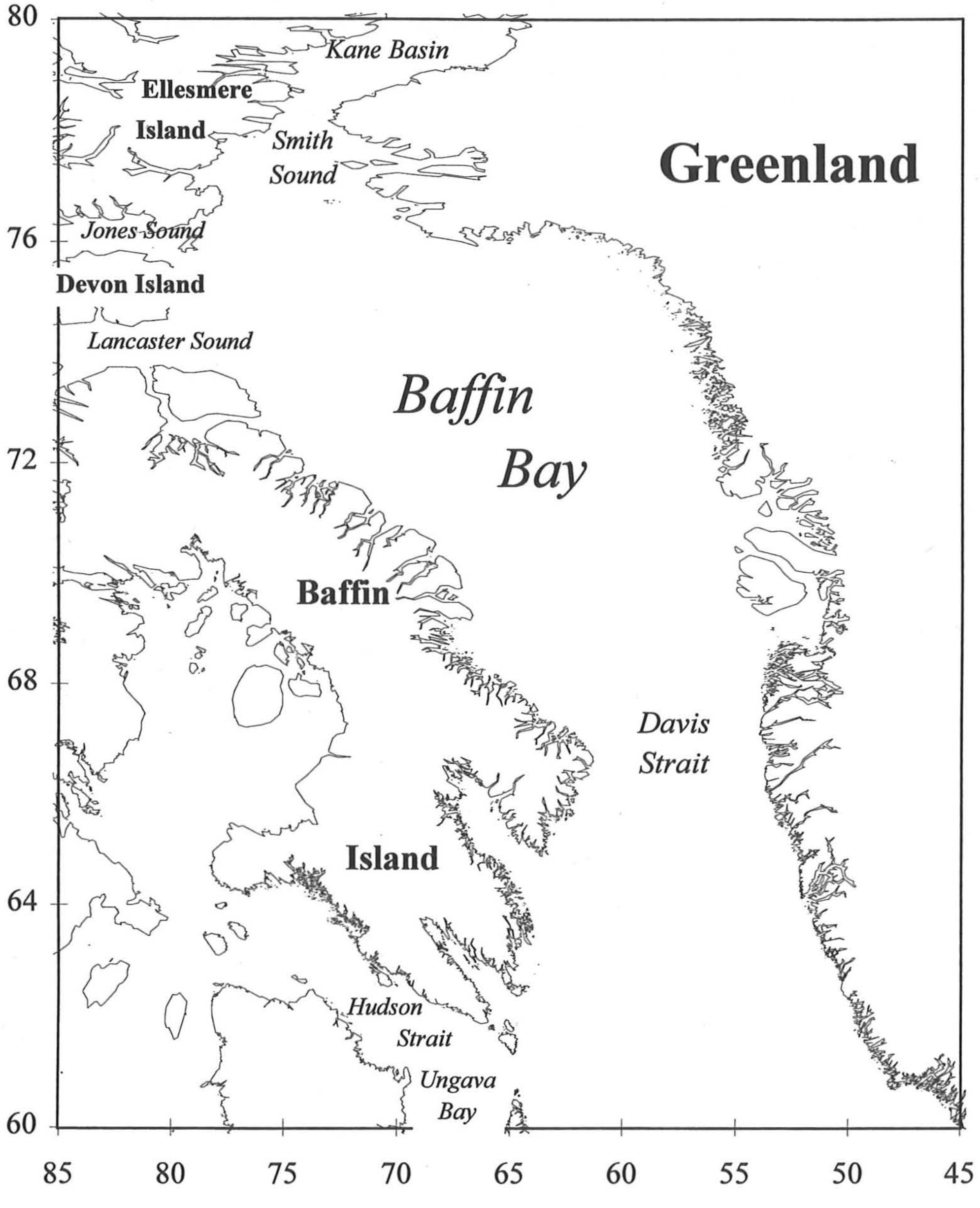

Fig. 1
Baffin Bay and associated waters showing localities mentioned in the text.

METHODS

Three linked spreadsheet models were built (using Excel®) to relate polar bear and seal populations. One model was of polar bear growth and energy needs, one was of polar bear population structure and the third was of ringed seal body mass and mortality against age, furnishing an energetic yield to the predator (see Appendix for details on models).

Polar bear population model

The population model used discrete age classes. A three-month age class gave a tractable model with adequate resolution. Life history was modelled from the age of 0.25 years when cubs were considered to emerge from the den with their dam. Mortality was based on a three-factor "competing-mortality" model (Siler 1979). An exponentially decaying juvenile mortality was specified by the zero-age mortality (i.e. the annualised rate of mortality in the first quarter after emergence) and by the age at which it declined to an annual rate of 5%. An exponentially increasing senile mortality was specified by the "onset age", at which it reached 5% per year, and by the "longevity", at which it reached 100%. A "base mortality" was the same for all ages. Age-specific quarterly survival was the fourth root of the product of three survival factors, each calculated as the complement of an annualised mortality factor. Birth rates were compounded of an age-independent mean litter size multiplied by an age-independent mean litter interval and an age-specific maturity factor. The sex ratio at birth was taken as unity. Birth rate and longevity parameters were fitted to existing population dynamics models (M. Taylor pers. comm.) and the juvenile mortality parameters were adjusted for a stationary population (Table 1). The number of bears in the population was taken as the average number over the year, as bear population estimates are not seasonally defined. This model of population dynamics was used to calculate the structure of a stable population, so that the energy requirements for growth and maintenance of the average bear could be estimated from an energy model.

Polar bear energy model

Body mass for cubs and yearlings were taken from the literature (Derocher and Stirling 1996) and verified by personal communication. A mass of 20kg was used for emerging cubs at age 0.25 years old, and 50kg for cubs in their first autumn considered to be 0.75 years old. For fall yearlings ("long" yearlings) a body mass of 110kg was used for males and 105kg for fe-

Table 1. Parameters of population dynamics models for polar bears and ringed seals using Siler-type (1979) competing-hazard mortality models.

	Polar bears		Ringed seals	
	Males	Females	High juvenile mortality	Low juvenile mortality
Initial mortality (%)	35	35	60	30
Age with 5% juvenile mortality (yrs)	4.81	4.31	5	3
Base mortality (%)	8.0	5.5	1.76	9.26
Age with 5% senile mortality (yrs)	16	16	16	16
Longevity (yrs)	24	24	24	24
Litter size		1.8		
Litter interval (years)		2.7		
Birth-rate multiplier		22.5% at age 5, 1 thereafter		
Basic birth-rate (seals/seal/yr)			0.46	
Mean age at 1st birth (years)			6.9	

Table 2. Parameters of growth curves for polar bear and ringed seal body mass for energetics modelling.

	Polar bear mass (kg)		Ringed seal mass (kg)
	Males	Females	
Initial size	20	20	17
Initial growth rate (/yr)	50	50	6.25
Asymptote	465	194	74
Richards shape parameter	0.35	0.55	0

To check the ringed seal mass-growth curve (fitted to age-mass data from McLaren 1958), published mass-length relationships (Ryg *et al.* 1990, Lydersen *et al.* 1992) were applied to an asymptotic growth curve fitted to age-length data in Smith (1987). McLaren's data agreed (±2kg) with Ryg's results between 0.25 yrs and 10.25 yrs, and with Lydersen's from 14.5 to 20 yrs.

males and from three years on, mass was taken from growth curves (Kingsley 1979). Richards (1959) curves were then fitted by eye to these sets of points by adjusting the parameters (Table 2). Maintenance energy for the age class was estimated from Kleiber's (1975) formula, using a conservative multiplier of 2.4 (selected near the minimum of the range of values - from about 2.3 to 4.4 - for eutherian mammals found in the literature) to convert basal metabolic rate (BMR) calculated according to Kleiber's model to an average active metabolic rate ("Field Metabolic Rate" or FMR) (cf. Nagy 1987, Markussen *et al.* 1990, Ryg and Øritsland 1991, Lydersen and Hammill 1993). Growth in body mass was calculated from the difference in mass between age classes, and growth energy of 31.4MJ per kg of growth was applied (Markussen *et al.* 1990). Energy needs that were processed through the female, i.e. through pregnancy or lactation, were assessed a premium of 20%, estimated as 15% assimilation loss for an extra stage of assimilation, and 5% milk production cost (Stewart and Lavigne 1984). The cost of maternity was estimated at five times this for the newly emerging cubs to cover the energetic costs of pregnancy. For the first year of life, all energy, for maintenance and for growth, was considered to pass through the mother, i.e. cubs met 100% of their needs from milk, so all these energetic needs were subjected to the maternity cost factor. The model then assumed a linear decline of the milk proportion to weaning at age 2 yr, i.e. after that age the young fed directly on seal and took no milk. Assuming a linear decline in milk intake starting at age one, the nursing rates of Arnould and Ramsay (1994) predict weaning at age 2.13 yr. Overall assimilation factor, i.e. the ratio of "metabolisable energy" to "gross energy" was taken the same for milk and for seal meat and blubber at 85%.

In this formulation, energy needs for producing and rearing male offspring were presented in the "Male" part of the model. In reality these energy needs represent energy taken from a seal population by, and passed through, the dam. In many conventional energy models this would be included in the energetic needs of adult females for pregnancy and lactation.

The product of the age- and sex-specific energy needs and the population structure gave an average energy need per bear in the population.

Seal population model

In ringed seals, the sexes do not differ much in size, and there is little information that they have different mortality factors or rates. Hence only one sex of ringed seal was considered. Three "competing" mortality components (Siler 1979) were used (Table 1). The same pattern of senile mortality was used as for polar bears, i.e. exponentially increasing to 5% at 16 years and 100% at 24 years. Birth rate was the product of an age-independent base rate of 0.46 per year and an age-specific maturity. A Gompertz curve was fitted to natality data in Smith (1987) to generate the age-specific maturity multiplier; the mean age of first birth was 6.94 years (Kingsley and Byers this volume). The "base mortality" parameter was adjusted for a stationary population. The population size parameter was estimated at the time when aerial surveys are usually flown, i.e. in the spring soon after the whelping season.

Seal growth model

Body mass at age for ringed seals was deduced from an estimated weaning mass of 20kg which was considered to be at age 0.25 years (Hammill *et al.* 1991). Yearlings taken at Sachs Harbour in the open-water hunting season in 1989 had an average mass of 24.7kg (Kingsley and Byers this volume). Adults 4+ years old taken at Sachs Harbour in 1989 had an average mass of 48kg, but adult ringed seals reach larger masses than this (Smith 1987, Ryg *et al.* 1990). A Richards growth curve fitted to age-mass data (McLaren 1958: his Appendix Table I) predicted a mass of 20kg at 6 months and 50kg at 8 years and was used to predict masses at all ages over 3 months. Alternative age-mass relationships were also calculated from a von Bertalanffy (1932) growth curve fitted to age-length data from Smith (1987). This was combined with published length-mass equations (Ryg *et al.* 1990, mean of male and female curves; Lydersen *et al.* 1992: their Fig. 1) and it agreed adequately with the former growth curve (see note to Table 2). Seal pups at zero age were considered not to be predicted by the growth curve but were assigned a mass of 5kg (Hammill *et al.* 1991, Lydersen *et al.* 1992). The mean mass of predated seals in an age bracket was taken as the mean of the starting and ending mass.

The energy content of ringed seals was calculated from Stirling and McEwan (1975) by regressing total energy against mass to obtain an energy-mass relationship of 19.7MJ/kg - 50 MJ.

Predation model

The simplest predation model was simplicity itself: all seal deaths were taken to be polar bear food. The mass of the seals dying from the population was converted using the mass-energy relation to an energetic yield to the polar bear population. The effects of other forms of mortality, such as predation by Arctic foxes (*Alopex lagopus*) on new-born pups or sub-adults dying from intra-specific hostility were considered by including an age-specific loss factor; i.e. the yield to the polar bear population was only a proportion of the deaths in the age class; waste, i.e. bears killing seals but eating only part of the carcass, were included in the same loss factor. This factor was arbitrarily set at 30% in the first three months, when bears may eat only the heads of white-coated pups, and when Arctic foxes may kill some pups; 20% from then until 2 years of age, and 10% thereafter. It has an important effect on the predator-prey modelling, but the existence and rate of non-polar-bear-caused mortality in ringed seals has not been well studied.

RESULTS AND DISCUSSION

Polar bear models

The estimate of early mortality rate and of the base rates for adult mortality used here (Table 1) were those used for management modelling (M. Taylor pers. comm.). The stationary population structure is shown in Table 3. Males were fewer in all age classes, but so much heavier than females that their total weight was greater

Table 3. Age and sex structure of a modelled stationary polar bear population.

	by mass		by number	
	Females	Males	Females	Males
Dependent young (to 2.5 years)	6.1%	6.2%	16.5%	15.9%
Independent juveniles (2.75 to 4.75 years)	7.2%	8.5%	8.7%	7.6%
Adult (5 years and older)	29.9%	42.1%	30.5%	20.9%

at all ages. Stirling and Øritsland (1995) modelled a population with lower birth-rates (0.449 cubs/female/yr, about 2/3 of the value of 0.667 used here) compensated by 90-93% survival of young. This gave a standing population with fewer young or old bears, but heavily weighted in the centre of the age distribution, i.e. the older sub-adult and younger adult classes. This may be due to the use of field data, possibly somewhat biased by the accessibility of various age classes, to derive the population structure.

Polar bear growth model

Parameters of the body mass growth models that best fitted the data are given in Table 3. The asymptotic mass used for females was taken from Kingsley (1979) and was similar to that used by Stirling and Øritsland (1995), and the resulting growth pattern is close to theirs. Females reached 90% of the mature mass at 4.5 years. The population mean mass for females was 152kg for the modelled population *versus* 153kg for Stirling and Øritsland (Ibid). The male asymptote was about 10% higher than theirs, so although mass at young ages were similar, the curves diverged at about 10 years of age. By that age, however, 5 of 6 males are dead, so in spite of this difference the modelled mean male mass, 250kg, was similar to that of Stirling and Øritsland at 251kg. The mean mass for all bears in the modelled standing population, 195kg, was close to the mean mass of 200kg used for energetics calculations by Kingsley (1990a). The sensitivity of the results to changes in population dynamics parameter assumptions was small.

Polar bear energetics model

The basic energetics model had the following parameter values: FMR was 2.4 times BMR; net assimilation was 88%; growth needed 31.4MJ/kg of assimilated energy; the basic "maternity premium" was 20%. With these values, and the population structure derived from the population dynamics model, the average energy needed was 19,580MJ ingested per male bear per year and 13,550 per female, or 16,230 ingested for the average bear in the population. Stirling and Øritsland (1995), with FMR=2, calculated 9,860MJ assimilated per bear-year. However, they tabulated energy needs for bears in their first four years of life that were half what they should be. When those values were doubled, their population average annual energy need became an estimated 11,020MJ/bear/year. They also modelled an "ideal predator" that eats all it kills, digests all it eats, grows without food, and has an average FMR no higher than twice its Kleiber estimate of BMR. For comparison, when the parameters of the present model were set the same, i.e. FMR/BMR=2, no maternity premium, no assimilation loss, and no growth needs; the result was 12,850MJ per male and 9,070 per female, and the average over a population with balanced sex ratio was 10,960MJ/year.

The additional factors considered in the present model altered this. The unbalanced sex ratio due to higher male mortality reduced the average by 2% to 10,750, but allowances for growth and maternity increased it again by 12% to 12,080. The largest factors, the value of 2.4 used to convert BMR to FMR and the assimilation factor, increased the needs again by a further 34% to an average ingested energy per bear of 16,230MJ/year; overall 63% higher than the estimate of Stirling and Øritsland. Kingsley (1990a) used a single mass of 200kg per bear, and applied a single factor of 4 to the estimated BMR to include assimilation, waste, and the FMR/BMR ratio, giving 22,740MJ killed per year.

The sensitivity of average energy needs to the values of the parameters in the energetics model was tested by changing the parameters by 10% and resetting the model. Changing either the assimilation factor or the FMR multiplier by 10% gave close to a 10% change in the annual ingested energy need. Reproductive rates, mother-cub energy transfer, and growth energy calculations had little effect on total population energy needs, because in the modelled stationary population most energy intake was used to maintain adults. As polar bears have low birth-rate, but high survival, growth (at 31.4MJ per kg) used only 8% of the ingested energy, and changing the growth-energy parameter by 10% altered the average energy need by only 0.8 %. A 10% decrease in birth-rate, compensated by a decrease in female base mortality, increased the average ingested energy needed per female by 0.7%. (An increase because the combination of lower birth-rate and higher survival resulted in fewer small animals in the population, so the average female was older and 1.5% heavier, and needed more energy for maintenance.)

Assimilation efficiency for polar bears feeding on seals may be similar to, or higher than, those of seals feeding on oily fish. Mean assimilation of energy was estimated at about 92.6% for grey seals (*Halichoerus grypus*) feeding on herring (Ronald *et al.* 1984), before subtracting urinary energy loss of about 8% of gross intake to leave a net assimilation of metabolisable energy of 82.7%. Stewart and Lavigne (1984) considered milk assimilation efficiencies of 80% (p. 189) and of 90% (p. 190) for nursing harp seal pups. Best (1977) gives overall assimilation of about 92% for polar bears.

Bears may eat only the fat of seals (Stirling 1974, Stirling and McEwan 1975, Stirling and Archibald 1977), and while in that case waste would be greater, assimilation efficiency may be as high as 98% (Best *loc. cit.)* of ingested energy. Ronald *et al.* (1984), however, estimated assimilation efficiency of lipid at only 92.7%. The range of estimates of net assimilation efficiencies appears to lie between 83% and 93%, i.e. the range of uncertainty is about ±5.7 % of the central value and translates into a component of uncertainty of the ingested energy needs of equal value.

The estimation of the actual average metabolic rate is more uncertain. The exponent used in the relationship of metabolic rate to body mass for adults, 0.75, was applied also to the growing young, although BMR for growing young marine mammals has been estimated at greater values (Lavigne *et al.* 1986). However, in this model an explicit growth-energy requirement for the young of 31.4MJ/kg has been included. Estimating an FMR/BMR ratio for free-ranging bears averaged over activities, seasons, sexes, and ages is a daunting proposition. FMR/BMR ratios to be found in the literature, some of which apply to specific activities over short periods, range from a little below 2 to about 6. An annual energetics model of ringed seals (Ryg and Øritsland 1991) estimated gross energy intake for adults (including reproduction costs) at 2.8 to 4.4 times BMR. Among the inputs to that model, however, were multipliers of 1 to 8 times BMR for the metabolic cost of swimming. Lydersen and Hammill (1993) estimated FMR of ringed seal pups in water at up to 6.4 times BMR. The FMR/BMR ratio assumed in any energetics model is important, having a directly proportional effect on any estimate of energetic needs, and yet it is difficult to measure except in the short term, and under favourable circumstances. Review of the available estimates indicates that the value of 2.4 used here is at the low end of the range of likely values.

Seal growth and population model

The standing population of seals to maintain one average polar bear was calculated from the annual energy need of the bear, the energetic yield per seal pup born, and the productivity of the seal population. Seal population productivity has been shown to vary, probably in response to ecological factors such as food supply affecting the age of first reproduction in females. Under good conditions, females may have a mean age of first birth of 5.4 years (Kingsley and Byers this volume). The reproduction ogee used in the present model was fitted to data obtained in a long-term study that may have included a diversity of conditions, and gave a mean age at first birth (6.9 years) greater than the minimum at which ringed seals are capable of reproducing. I.e. the reproductive capability used in the present model is not that of a maximum-yield population density, but rather of a long-term average replacement yield.

The energetic yield per pup born varied with the mortality structure. Two mortality structures were used. They were chosen to be extreme, so as to include between them the range of possible likely values. A high-juvenile-mortality scenario had an annualised rate of mortality of 60% at age zero, and juvenile mortality did not fall to 5% until 5 years of age. This was compensated for stationarity by an annual base rate of mortality of only 1.76%. The low-juvenile-mortality scenario had an initial mortality of 20% which decreased to 5% as early as age 3 years; however, base mortality for stationarity was then 9.26%. Estimated energy content at age varied from about 314MJ at 3 months to about 1,381MJ at asymptotic mass. When most mortality was on young seals (60% first-year mortality), the energetic yield was 536MJ/birth; when first-year mortality was low (20%), but adult mortality high, the energetic yield per birth was 26% higher at 678MJ. With no waste factor, therefore, an average bear would need 24 seals per year if there was high predation on adults, or 30 if the pups were being heavily predated.

It has been thought that ringed seal populations withstand polar bear predation because bears mostly take young pups (Smith 1980, Stirling and Øritsland 1995). In the present model, the estimated population required to support one bear was about the same. The estimate is independent of whether the predation on pups was high or low. With high pup mortality it took (with no waste) a population of about 136 seals to support a polar bear, but with low mortality it took 139. With high pup mortality and low adult mortality, the standing population of 136 seals (with a high proportion of adults) had an average birth rate of 0.22 and produced 30 pups. Seals taken by bears were mostly young and the yield per birth was 30kg; the annual yield to the predator was 900kg. When pup mortality was low and adult mortality high, the seal population (with a higher proportion of pups) was less productive, with an average birth rate of only 0.17, so 139 seals produced only 24 pups. But heavier seals were taken by the predator, and at 37kg per birth the yield was still 888kg per year.

These figures were insensitive to waste of pups, even when first-year mortality was high, moderately sensitive to waste of juveniles, and most sensitive to waste of adults, even when adult mortality was low. Other bears may scavenge parts of seals not eaten by the bear that killed it, so waste by the predator *population* may be quite low. Arctic foxes prey on new-born pups, sometimes at a high rate (Smith 1976), but the effect on the bear:seal ratio of such predation was small: if first-year mortality was set at 60%, of which 60% was wasted (e.g. pups killed by foxes), the standing population was still no higher than 142 seals per bear compared with 136 with no waste. The mean utilisationís in samples of bear-killed seals observed in different areas of the Arctic and different years ranged from about 60% to about 90%. The waste parameter set here, 10%, is at the low end of that range.

From an observed distribution of predation between seal age classes (their Table 2) and assumed energetic values (p. 2597), Stirling and Øritsland (1995) show an average energetic value of 364MJ/kill. When compared with an average FMR of 11,021MJ/bear/year (their Table 3 and above) this indicates 30.3 kills per year, within the range calculated above. Their energetic values for seals are lower than those used here, but their FMR values for bears are also lower and they include no growth requirements. If their average 364MJ/kill is divided into the energy need of 16,146 MJ/bear/year produced by the present model, the estimate is 44.5 kills/year. Their field estimate is 43 kills/bear/year. This is based largely on summer data, but is insensitive to the assumptions made about kill rates at other seasons. It is, however, largely based on observations at a single site.

From these energetic and population models, an accessible population of about 140 ringed seals is needed to maintain an average polar bear if kills are not wasted. This estimate is sensitive to metabolic factors, but not to the age class of seals predated or to the structure of the polar bear population. With a little waste, or take by other predators, standing population ratios rise to about 160-170 seals/bear. This is not sensitive to waste of new-born pups, but to the more energy-rich older age classes. If energetic yields per seal were lower, as suggested by Stirling and Øritsland (1995), the required standing population would be 30% higher, or about 180 seals per bear with no waste, 215 with some waste.

In summary, there are three main differences between the present modelling approach and that of Stirling and Øritsland (1995). 1) The present model uses a population dynamics model to derive the age structure of the polar bear population, while Stirling and Øritsland have used an age structure, that is based on observational data, but even so is somewhat improbable. This is unimportant and does not greatly affect results. 2) Stirling and Øritsland have modelled a highly efficient predator that wastes nothing and needs little energy for growth or activity, so all ages need to ingest only 2 times the Kleiber estimate of BMR. As they point out in their discussion, this is perhaps idealistic. The present model includes allowances for growth, inefficient assimilation, inefficient predation (waste), and less efficient activity (FMR is 2.4 times BMR). 3) Stirling and Øritsland's efficient predator fed, however, on rather low-energy seals, with a mean energy of only 364MJ/kill. Their predation pattern on ringed seals is so heavily weighted toward the younger age classes that it is difficult to construct a stationary population without introducing a separate cause of adult mortality; this would, however, alter the standing population ratios. Also, their mean energy content of adult seals (628MJ for a mean adult mass of 44kg) is only equivalent to 14.2MJ/kg. The present model, even when pup mortality is high, produces a mean energy per kill of 536MJ.

The second and third of these differences roughly compensate, and both models estimate standing population ratios of about 150 seals/bear. It seems possible, however, that Stirling and Øritsland's model under-estimates ingested energy needs, the present model over-estimates energy content of killed seals, and both models underestimate the effects of waste, other predators, and other causes of death, so standing population ratios are more likely to be underestimated than overestimated.

Polar bear population estimates

Polar bear population sizes in Baffin Bay and associated waters, with the evaluated quality of the population data were: 2,200 ("good") in Baffin Bay, 1,200 ("fair") in Davis Strait, 200 ("fair") in Kane Basin, and 1,700 ("good") in Lancaster Sound (GNWT 1997). The Lancaster Sound polar bear management region includes Jones Sound, but it extends westward in the Parry Channel as far as 110°W, and so only 25% of the bears in it were considered to utilise the ringed seal population of Baffin Bay. The total was 4,025. At 150–200 seals/bear (a ratio that includes wastage), a standing population, accessible to bears, of about 0.6–0.8 million seals would be needed to maintain them, yielding 18–22%/year or about 120,000 to 160,000 seals killed per year.

When ringed seal populations have been in poor condition and reproductive rates low, the effects on polar bear populations have been marked and immediate, as though bears are quite dependent on ringed seals with few alternatives readily available (Stirling and Lunn 1997, Kingsley and Byers this volume). However, polar bears take other prey, of poorly quantified energetic importance. They are known to prey on bearded seals (*Erignathus barbatus*) (Smith 1980), but there is no estimate of how much, and there is little information on populations of this species. Bearded seals are mainly found in loose-ice areas over shallow water (Smith 1981, Kingsley *et al.* 1985). Over much of the high Arctic they are much less abundant than ringed seals (e.g. about 1:20 in the Beaufort Sea, Stirling *et al.* 1982; 1:60 in the high Arctic survey area, Kingsley *et al.* 1985). These characteristics may limit their importance in the diet of polar bears, especially in areas of mostly deep water such as Baffin Bay. Polar bears also scavenge, and sometimes prey on, belugas (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) (Freeman 1973, Sergeant and Williams 1983, Lowry *et al.* 1987a, Smith and Sjare 1990, Kingsley 1990a, Rugh and Shelden 1993). Each species, numbering in the very low tens of thousands in Baffin Bay and associated waters (Koski and Davis 1994, Richard *et al.* 1994, S. Innes unpublished data), probably represents a resource biomass of the same order of magnitude as the ringed seal population. Predation in the summer open-water season occurs, but is apparently slight and opportunistic (Smith and Sjare 1990). Monodontids crowded into small openings in ice, whether absolutely trapped or not, are the commonest prey referred to. Lowry *et al.* (1987a) indicate that on some parts of the spring migration routes of belugas in the Alaskan Arctic, polar bears may be able, in most years, to hunt belugas moving freely through narrow leads. The energetic advantages for bears would be substantial, but similar hunting opportunities have not been reported for the Baffin Bay region. There are also other marine mammals, such as harp (*Phoca groenlandica*) and hooded (*Cystophora cristata*) seals which pup on moving ice within the range of the bear populations considered here. Polar bears have been observed among both whelping harp and hooded seals. The lack of ecological studies and quantitative information on the relative importance of prey other than ringed seals is a serious problem in trying to examine this predator-prey relationship.

Inuit hunters in communities in Baffin Bay take an estimated 100,000 seals per year (Teilmann and Kapel this volume, Reeves *et al.* this volume). At a sustainable yield of 20% per year, a standing population of about 0.5 million seals is required to sustain this harvest. The total standing population to sustain the two main predators is therefore estimated at about 1.2 million seals. If the population is partly inaccessible to the predators, it may be larger. This is a rough estimate, which depends on at least three parameters (Field Metabolic Rate; bear population size; and the predator-prey link including food habits and wastage) which probably have individual error CVs in at least the 10 -20% range, so their compounded SE would be 17 - 34%.

Other species that have been reported, or suspected, of catching ringed seals include wolves (*Canis lupus*), wolverines (*Gulo gulo*), grizzly bears (*Ursus arctos*), walruses (*Odobenus rosmarus*), and killer whales (*Orcinus orca*). Of these, the terrestrial species can be considered incidental or opportunistic and unlikely to affect population numbers. Walruses may locally affect the distribution of ringed seals and may tend to exclude them from some areas of otherwise suitable habitat, but active predation probably has a small effect on the overall populations. Ringed seals seem to fear killer whales, those near the coast hauling out on land when killer whales are near. Predation on ringed seals has been confirmed from examinations of killer whale stomachs (Jefferson *et al.* 1991) and from Greenland unspecified seal remains have been reported in killer whale stomachs (Heide-Jørgensen 1988). Field observations do not mention attacks on ringed seals (Lowry *et al.* 1987b, Heide-Jørgensen 1988), but are usually made in summer when ringed seals are hard to see. Although few killer whales have been seen in systematic marine mammal surveys of Davis Strait and Baffin Bay, Reeves and Mitchell (1988) listed observations in north Baffin Island in 6 of 11 years from 1975 to 1985. Also, killer whales have been sufficiently abundant to be considered a pest worthy of control measures, with observations of up to 90 killer whales, off West Greenland listed for most years in the 1980s (Heide-Jørgensen 1988).

Area estimates of ringed seal populations in Baffin Bay

Direct estimates of the size of the ringed seal population in Baffin Bay were made by dividing it into different regions, estimating the areas of different kinds of ice in each region (Miller *et al.* 1982), and referring to published results of aerial surveys for ringed seals for likely density values in different ice types.

The density classes considered were fjord fast ice, shelf fast ice and stable pack ice (Table 4). Fjord fast ice was considered to have the highest densities. Miller *et al.* (1982) indicate mean densities in fjord ice for all the Baffin Island and West Greenland coasts of Baffin Bay of about 2.1 seals/km^2, uncorrected for detection bias of about 32% or for availability bias (Koski 1980). Correcting for detection bias would raise this to about 2.8 seals/km^2, which would put it among the highest densities recorded for ringed seals in fast ice. Densities in Amundsen Gulf, probably not all resident seals, were 2 to 3.5 seals/km^2, in a productive area of the western Canadian Arctic (Kingsley 1986). Densities in high Arctic areas (Smith *et al.* 1979, Kingsley *et al.* 1985) were almost all less than 1 seal/km^2. A density of 2.0 seals/km^2 was therefore assumed for fjord fast ice. Shelf fast ice in Jones Sound and Kane Basin was assigned a density of 0.33 seals/km^2 (Kingsley *et al.* 1985), and in West Greenland and western Baffin Bay 1.3 seals/km^2 (Miller *et al.* 1982). Stable pack ice in Baffin Bay of 5/10 cover and greater was estimated to have a density of about 0.85 seals/km^2 (Koski 1980 cited in Miller *et al.* 1982: 0.64 corrected by 32% for detection bias). However, Miller *et al.* (1982) point out that aerial surveys conducted at an altitude of 50m may underestimate seal densities, and Finley *et al.* (1983) estimated the pack ice population at about double this. The density in the pack ice was assumed to be 0.85 times 1.5, i.e. about 1.3 seals/ km^2 and the same density was assigned to the Ungava Bay pack ice as well. Ringed seal habitat in southern Baffin Island (south of Cape

Table 4. Ice areas and estimated seal numbers in Baffin Bay and associated waters.

	Fjord fast ice		Shelf fast ice		Stable pack ice		
Region	Area ('000km^2)	Number ('000)	Area ('000km^2)	Number ('000)	Area ('000 km^2)	Number ('000)	Total
Jones Sound			21.0	6.9			6.9
Kane Basin			18.5	6.2			6.2
East Devon & East. Ellesmere islands	5.3	10.6					106.
Eclipse Sound and associated waters	8	16					16
West Greenland	40.6	81.2	10	13			94.2
West Baffin Bay	16.1	32.2	20	26	301	391.3	449.5
South Baffin Island	25.2	50.4					50.4
Ungava Bay	6.4	12.8			25.1	32.6	45.4
Total hauled out		203.2		52.1		423.9	679.2

Areas: Fjord fast ice from Miller *et al.* (1982): their Table 1; Jones Sound from Miller *et al.* (1982) p. 6 considered shelf ice; shelf ice in Baffin Bay from Miller *et al.* (1982): their Table 5; pack with 60%+ ice cover from Miller *et al.* (1982) p. 31 and from measurements;
Densities: fjord fast ice 2 seals/km^2; shelf fast ice in Jones Sound and Kane Basin 0.33 seals/km^2 (Kingsley *et al.* 1982), in West Greenland and in West Baffin Bay 1.3 seals/km^2 (Miller *et al.* 1982: their Table 5 uncorrected); stable pack ice 1.3 seals/km^2.

Dyer) was estimated to comprise 25,200 km^2 of fjord fast ice, and Ungava Bay was estimated as having 6,400 km^2 of fast ice and 25,100 km^2 of stable pack ice that could constitute habitat for ringed seals.

The resulting estimate of total survey-sightable seals is about 680,000, of which 58% are estimated to be in the Baffin Bay pack ice (Table 4). Estimates of the maximum proportion of ringed seals hauled out have ranged from about 50% (Smith and Hammill 1981) to about 70% (Finley 1979). The upper end of this range may, from the behavioural aspect, be more likely. Although this does not imply that it furnishes an adequate correction factor for the average aerial survey flown under average conditions, it is, nonetheless, used here. A paired photographic and visual survey, flying two aircraft simultaneously over the same transects, indicated that visual observers detect about 80% of the hauled-out seals counted by photography (Kingsley unpublished data). Correcting the estimate of 0.68 million sightable seals for these availability and detection biases yields a population estimate of about 1.2 million, which is within the range of populations estimated as necessary to sustain the combined predation and human harvest.

The critical components in this analysis are the ecology of polar bears, including their annual average Field Metabolic Rate and the composition of their diet; the population energetic yield of ringed seals to polar bears, including allowances for the impact of other predators; and the true density of ringed seals in the Baffin Bay pack ice. The physiological parameters of polar bears, including assimilation efficiencies, efficiency of energy transfer in reproduction and nursing, and the energy cost of growth, seem less critical. Polar bears and ringed seals can interact under a range of conditions in which research studies, whether of metabolic rates or of predation patterns, are difficult to execute. The density estimates used here have been on the low side of the estimates for the Baffin Bay region suggested by Miller *et al.* (1982) for fast ice, but the fast ice areas only hold 42% of the estimated seal population. The density assumed for ringed seals inhabiting the large area of dense pack ice in Baffin Bay has a large influence on the estimate of population size.

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Appendix: Model formulation

This Appendix provides detail of the model structures to complement and complete the narrative descriptions in the text of the article

A. POLAR BEAR POPULATION MODEL

The polar bear population model had a panel for each sex. Mortality was composed of three components: juvenile mortality, base mortality, and senile mortality. Juvenile mortality, exponentially declining with age, was given by:

$$J_x = J_{x_o} \,.\, \exp\left[-\left(3+1\mathrm{n}\, J_{x_o}\right) \cdot \left(x-x_0\right)/x_{J5}\right]$$

where $\boldsymbol{J_x}$ was annual juvenile mortality at age $\boldsymbol{x}$ yr, $\boldsymbol{x_0}$ was the age of the first age-class (0.25 years for polar bears) and $\boldsymbol{x_{J5}}$ was the age at which annual juvenile mortality declined to 5%. Annual base mortality $\boldsymbol{B}$ was a constant. Senile mortality was given by:

$$S_x = \exp(-3\ (L-x)/(L-x_{S5}))$$

with a maximum at unity, where L (yr) was the longevity and x_{S5} the age at which annual senile mortality passes 5%. Three-month survival was calculated as:

$$P_x = \sqrt[4]{(1\text{-}J_x).(1\text{-}B).(1\text{-}S_x)}$$

The number in the first age-class was set equal to 1, and the number N_x in each succeeding age class was obtained by multiplying by $P_{(x-0.25)}/((1+\lambda)\char`^0.25)$, where λ was the population growth rate (assumed zero).

Birthrates m_x (cubs/female/year) for female polar bears were produced by multiplying 3 factors, a mean litter size **Z** (set to 1.8 cubs/female/litter for all ages), a mean interval between litters **I** (2.7 yr/litter for all ages), and an age-specific relative natality M_x (0.225 at age 5.0, 1 at all greater integer ages, 0 at all fractional ages). Production was obtained by multiplying the number of females in each age-class by its birthrate. Other parameters were set to the values of Table 1, and the model was closed by adjusting the female x_{J5} until the total production equalled 2, the size of the 0.25-yr age-class for the two sexes combined:

$$\sum_{x=integer} Z\,I\,M_x N_x = 2$$

The value of $J_{0.25}$ was set the same for the two sexes, but x_{J5} was set 0.5 yr greater for males than for females, on the assumption that among older juveniles, males have higher mortality than females.

The number of bears in the population was calculated from the sum of N_x for all the three-month age classes from 0.25 yr to 24, divided by 4.

B. POLAR BEAR GROWTH MODEL

Estimated weights from the von Bertalanffy curves of Kingsley (1979) and from Stirling and Øritsland (1995) were averaged for ages 3 and above, and the literature and personal communications were used as sources for estimated masses for young bears of 20 kg at age 0.25 yr, 50 kg at age 0.75 yr, and 110 kg at age 1.75 yr. A Richards growth curve:

$$w_x = W_\infty\left[1\text{-}\left(1\text{-}(w_{0.25}/W_\infty)^{1\text{-}m}\right).\exp\left(\frac{-\,(x\text{-}0.25)\,k_{0.25}\,(m\text{-}1)}{w_{0.25}\left(1\text{-}(w_{0.25}\,/\,W_\infty)^{m\text{-}1}\right)}\right)\right]^{(1/(1\text{-}m))}$$

was then fitted to these composite data sets, where w_x is the weight (kg) at age x yr and k_x is the rate of weight change, m is a shape parameter for the curve. The parameters of the curves are given in Table 2.

C. POLAR BEAR ENERGETICS MODEL

There were two components to energy needs: maintenance energy and growth energy. Maintenance energy was based on Kleiber's formula, using the age-class weight, with a constant factor to convert BMR to FMR; growth energy was the weight gained to the next class, with a constant factor for unit growth energy need. Two corrections were applied: for assimilation efficiency, and for milk production and other reproductive costs.

$$E_x = \left(\frac{365}{4}\,.\,2.93\,.\,w_x^{0.75}\,.\,F + (w_x - w_{x\text{-}1}).G\right)\frac{(1+M)}{A}$$

where E_x is the ingested energy need per bear (MJ per quarter) in age-class x, w_x is the weight of age-class ***x***, ***F*** is the FMR/BMR ratio (2.4 was used, considered conservative), ***G*** is the unit growth energy (31.4 MJ/kg), ***A*** is the assimilation efficiency (88%) and ***M*** is the maternity factor (set at 1 for the 0.25-yr age class, 0.2 for age classes 0.5 through 1 yr, and thence linearly decreasing to reach 0 for the 2.25-yr age class. The population energy need was the sum over sexes and age classes of the products of the age-class ingested energy need per bear and the number in the age class.

D. SEAL POPULATION MODEL

The seal population model was similar to that for bears, with the following differences:

- the first age-class was zero age;
- there was only one sex;
- base reproductive rate was not compounded of litter size and interval parameters, but was a single value (0.46 births per year per adult);
- age-specific birth-rate was a Gompertz curve,

$$M_x = \exp(-\exp(-e.k_b\,.\,(x-\mu+0.5) - 0.5772))$$

where μ is the mean age at first birth. Births only occurred at integer ages.

- juvenile and senile mortality parameters were set, and the model was subsequently closed by adjusting the base mortality rate until the total reproduction equalled 1.

E. SEAL YIELD MODEL

Seal mass at age was given by a Richards curve as above, with parameters in Table 2, except that the zero-age class was assigned a mass of 5 kg. The energy content at age ***x*** was calculated from

$$EC_x = U.w_x + V$$

where ***U*** (=19.7 MJ/kg) and ***V*** (=-50.2 MJ) were the parameters of a straight line fitted to data on weight and calorific value from Stirling and McEwan (1975). The energy yield to the predator from age class **x** was calculated from:

$$Y_x = \frac{(EC_x + EC_{x+1})}{2}(N_{x+1} - N_x)(1 - s_x)$$

where s_x was an age-specific waste factor set at 30% for age class zero, 20% for age-classes 0.25 through 2.0 yr, and 10% thereafter.