Estimates of energy expenditure and energy consumption of ringed seals (*Phoca hispida*) throughout the year

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We have employed a model for the energy balance of seals to estimate the energy consumption and energy expenditure of ringed seals throughout the year, using biological and physical parameters as input. Data on growth and seasonal changes in body mass and fat content "drives" the seasonal dynamics of the model output. The energy requirements for lactation and activity are based on data from earlier published studies.

The analysis suggests that the food intake of ringed seals is highly seasonal. In adult males it is low during the periods of territory defense, mating and moulting from March to June. During this period the seals lose body mass, mainly as fat. The model predicts that lactating females increase their food intake to some extent during the approximately six-week lactation period. After the ice breakup, food intake increases in both sexes, partly as a result of increasing maintenance energy requirements, and partly because the body fat stores are rebuilt in late summer and autumn. The over-all energy requirements of the ringed seal appear to be basically similar to those of terrestrial mammals.

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Introduction

The ringed seal (*Phoca hispida*) is the most abundant of the Arctic pinnipeds, with population densities ranging from 0.15 to 2.97 km^{-2} (Frost & Lowry 1981). It has a circumpolar distribution and is able to stay in ice-filled waters the year round because of its ability to keep breathing holes open in thick ice. This makes the ringed seal a potentially important predator in the Arctic marine ecosystem.

Two important aspects of the role of a predator in the ecosystem is what it eats and how much it eats. In this paper we investigate the latter aspect by estimating the energy requirements of individual seals, depending on their age, sex, and reproductive status, and then we extend our calculations to an entire, hypothetical, ringed seal population.

Like most pinnipeds, the ringed seal is a seasonal breeder. The pups are born in subnivean lairs in late March or early April (Smith & Hammil 1981; Lydersen & Gjertz 1986) and are suckled for about six weeks, an unusually long lactation period for true seals. Mating takes place sometime during lactation. The sexually mature males defend territories from the beginning of March until the end of the mating season. Moulting occurs in May and June, usually before the ice breaks up.

During the reproductive and moulting periods, the seals can spend a considerable amount of the time on the ice, although this depends on the weather (Smith & Hammill 1981). The adults lose body mass, mostly as fat, during these periods (Ryg et al. 1990). The sexually immature animals do not lose body mass, but body fat content may decline slightly during the spring to a minimum after the moult (McLaren 1958; Smith 1973, 1987; Ryg et al. 1990).

The seasonal changes in body mass and fat content have implications for the seals' energy requirements. Depletion of depot-fat will cover some of the animals' energy requirements, but this is a debt that has to be repaid by increasing food consumption later on to replenish the fat reserves. Also, the fat-filled subdermal tissues, called blubber, constitutes the main insulation of marine mammals; changes in body fat content may thus influence the energy costs of maintaining a constant deep body temperature. Here we use published information on seasonal variations in body mass and body composition, pup growth, thermoregulation, and behavior to calculate an annual energy budget for ringed seals. We conclude firstly that the consumption rate of ringed seals is highly seasonal, possibly an adaptation to a seasonally changing food base, and secondly that the annual energy consumption is not significanty different from that of a terrestrial mammal of similar size.

Methods

We calculated the energy requirements of ringed seals of different age classes and reproductive status as the sum of energy requirements for maintenance, growth, fattening and milk production. During periods of mass loss, energy consumption rates were calculated as the difference between gross energy requirements (assuming a metabolisable energy content of the food of 80%) and the energy supplied by the loss of body mass.

Maintenance energy requirements in water were calculated as the sum of basal metabolic rate (BMR) and the metabolic cost of swimming, or the minimum heat production required for thermal balance, $H_{min} = 11.4 \cdot c \cdot (\text{Body length}) \cdot \Delta T / \ln(\text{body mass/core mass})$ (Ryg et al. 1988), whichever was highest. We assumed a blubber conductivity (c) of 0.2 $Wm^{-1}{}^{\circ}C^{-1}$ (Scholander et al. 1950; Parry 1949) and ΔT of 30°C (Taugbøl 1982). We assumed that maintenance requirements in air were 1.5 times BMR. Basal metabolic rate was calculated as the "Kleiber metabolic rate", $BMR\ (\text{Watts}) = 3.39 \cdot BW^{0.75}$ (Kleiber 1975; Lavigne et al. 1986), except for pups, where BMR was assumed to be three (for the first two weeks) to two times Kleiber metabolic rate (Taugbøl 1982). The metabolic cost of activity was calculated as a multiple of the estimated BMR. Energy expenditure of free diving seals ranges from about 1.9 times the estimated BMR in harp seals (Øritsland & Ronald 1975) and Weddell seals (Kooyman et al. 1973) to about 3.5 times estimated BMR in harbour seals (Davis et al. 1985; N. H. Markussen, M. Ryg & N. A. Øritsland, unpubl. data). Here we assume that energy expenditure during diving in ringed seals is 2.5 times the estimated BMR. To account for activity of the pup, we assumed that their maintenance energy requirements were twice their BMR.

During lactation and moult the ringed seals spend a considerable amount of time on the ice. Smith & Hammill (1981) observed that individually identified seals emerged from the water from two to six times a day to haul out for periods ranging from one minute to over 10 hours. In one case a seal remained hauled out on the ice continuously for more than 40 hours. Lydersen (1991), by using telemetry, found that a ringed seal spent 55% of its time in water in late spring; 70% of the time in water was spent diving. Here we have assumed that the seals spend 55% of their total time in water during the period of ice-cover.

The energy requirements for growth and fattening were calculated by dividing the change in body energy reserves by the efficiencies for fat and protein synthesis. Webster (1983) showed that the energetic efficiencies of fat and protein synthesis were 74% and 44% of metabolisable energy intake when the diet consisted of protein and carbohydrates. The efficiency of fat synthesis from a high-fat diet will be higher, and we have assumed that the efficiencies of fat and protein synthesis were 90% and 44% respectively. These figures seem to agree reasonably well with over-all efficiency during feeding experiments on harbour seals (Markussen et al. 1990). Energy requirements for milk production were calculated as the sum of the change of energy stores of the pup (corrected for efficiency as above) and the maintenance requirements of the pup. Metabolisable energy content of milk was set to 90% of the gross energy. We assume that the pups grow at a rate of 0.42 kg/day throughout a 40-day lactation period, and that 60% of the mass gain consists of blubber. This growth rate is lower than the 0.76 kg/day suggested by Smith (1987), but it agrees well with a commonly found weaning mass of 22 kg (Hammill et al. 1991). We have used the difference in average energy intake during the periods of mass gain and mass loss, in percentage of the average energy intake, as a measure of seasonality.

The method we used to calculate mass changes was not sensitive enough to detect any difference between the females' mass losses during and after lactation. Differences in the timing of birth, with a resulting asynchronous lactation period, will lead to underestimation of the mass loss. We therefore assume that the average mass loss of 160 g/day in spring occurs entirely during the 40 days of lactation, giving a mass loss of 410 g/day during this period.

We extended the calculations for individual animals to a hypothetical ringed seal population

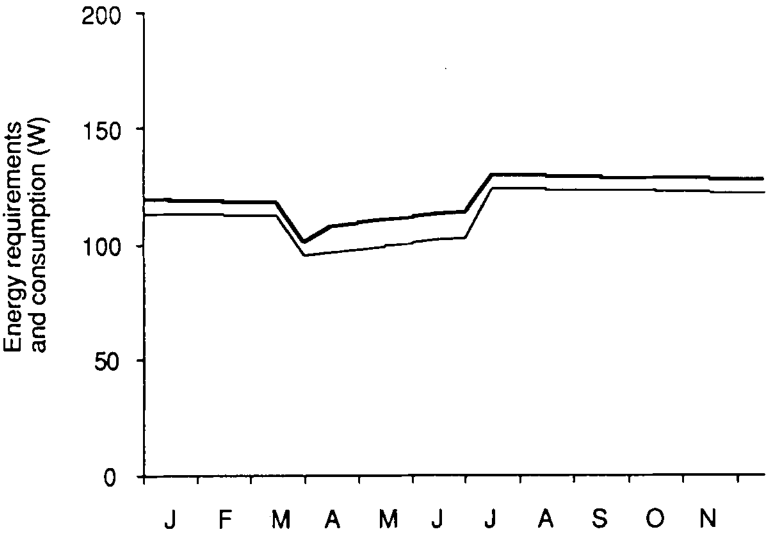

Fig. 1. Seasonal variations in maintenance energy requirements (thin line) and metabolisable energy consumption (heavy line) of immature ringed seals of age 3+.

with a stable age structure. The age frequencies were taken from the smoothed frequencies reported by Smith (1987) for Holman in the western Canadian Arctic.

The sensitivity of the outcome of the simulations with regard to total annual consumption and the amplitude of consumption rate was tested by varying the energy cost of diving and the amount of time spent on the ice during lactation and moult. The conclusions regarding the food consumption of lactating females were tested by varying the growth rate of the pups and the mass loss of the females during lactation.

Results

The simulations showed seasonal variations in maintenance energy requirements and consumption in both sexes and all age groups. The absolute and relative changes found in juvenile animals were less pronounced than in the adults and resulted primarily from variation in the length of haulout periods on the ice in the spring (Fig. 1). Seasonal variations in energy intake for the adults resulted primarily from the changes in body energy reserves and the costs of lactation.

The seasonal variations in body mass and body composition of the adult males led to a cyclic

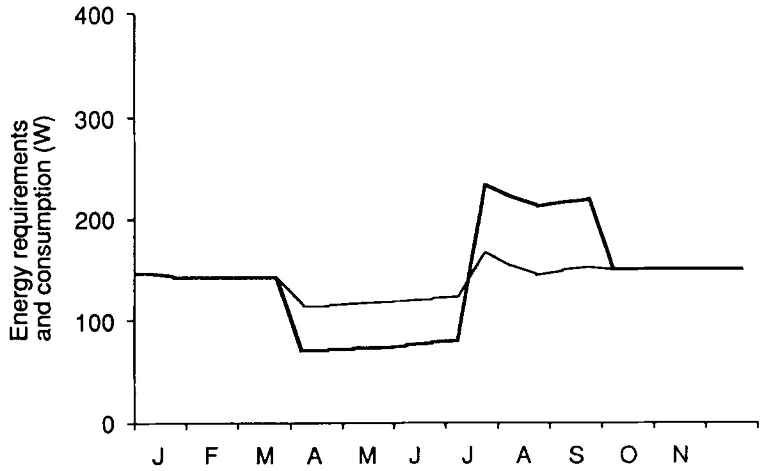

Fig. 2. Seasonal variation in maintenance energy requirements (thin line) and metabolisable energy consumption (heavy line) of adult males.

Table 1. Estimated metabolisable energy consumption (Watts) of lactating females as a function of female weight loss and pup weight gain.

Weight loss of mother, kg/day	Weight gain of pup, kg/day		
	0.36	0.42	0.76
0.16	329	364	552
0.42	212	246	434
0.62	128	162	350

pattern of predicted maintenance energy requirements and energy intake, with a minimum during the period April–June, and a maximum in July–October (Fig. 2). The annual gross energy consumption per adult male was $5.6 \cdot 10^9$ Joules, and the amplitude in the consumption rate, or difference in average food intake during mass gain and mass loss, was 103% of the mean annual consumption.

The estimated energy consumption rates for the adult females showed two peaks, one during lactation and one during the fattening in late summer (Fig. 3). The combined energy requirement for maintenance and milk production had its annual maximum during lactation. The estimated consumption rate during lactation depended on how the female's mass loss is partitioned between lactation and post-lactation, but it did not decline to zero for any combination of growth rate of the pup and mass loss of the mother (Table 1). The calculated annual consumption per adult female was $7.3 \cdot 10^9$ Joules, and the amplitude in consumption rate was 48%.

The energy consumption for a hypothetical population with a stable age structure had a pronounced maximum in late summer and fall (Fig. 4). The average consumption per individual in the population was $4.6 \cdot 10^9$ Joules gross energy per year, or 3.0 times the estimated BMR. Assuming an energy to carbon ratio in organic matter of 50 kJ/g carbon, this energy requirement corresponds to a biomass of 254 g carbon per day.

The figures for the average annual consumption were sensitive to the stipulated swimming metabolic rates but were not much affected by differences in haulout behaviour or rates of mass loss in spring. If we varied the swimming metabolic rate from one to eight times the estimated BMR (Ashwell-Erickson & Elsner 1983), the average gross energy requirements per individual increased from 2.8 to 4.4 times the estimated BMR. On the other hand, the amplitudes in consumption rate were largely unaffected by changes in swimming metabolism, but increased with increasing haulout time in spring.

Discussion

Depending on the setting of the parameters, the estimated mean annual consumption rate varied

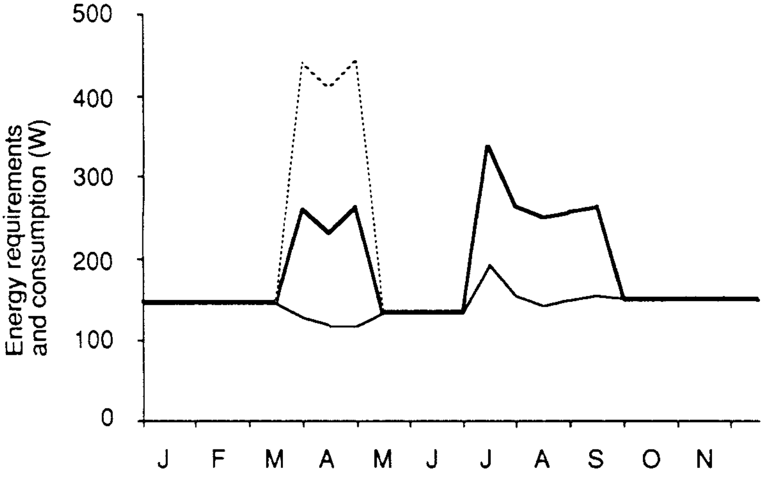

Fig. 3. Seasonal variations in energy requirements for maintenance (thin line) and milk production (dotted line), and metabolisable energy consumption (heavy line) of adult females.

Fig. 4. Seasonal variations in per capita metabolisable energy consumption of a hypothetical ringed seal population with a stable age structure.

between 2.8 and 4.4 times the estimated BMR. Nagy's (Nagy 1987) analysis of field metabolic rates of mammals included marine mammals. If one includes only the terrestrial eutherian mammals from Nagy's paper, the field metabolic rate is 2.8 ± 0.4 (mean ± 95% confidence limits) times the Kleiber level, independent of body size. For a metabolisable energy content of food of 80%, as used in the present paper, this metabolic rate corresponds to a gross energy intake of 3.5 ± 0.5 times the Kleiber level. Our estimates, ranging from 2.8 to 4.4 times the Kleiber level therefore suggest that the ecological energetics of the ringed seal is not significantly different from that of terrestrial mammals, thus supporting the analysis of Lavigne (1987) on the bioenergetics of pinnipeds. It should also be noted that our results agree with the old "5%-rule" (Sergeant 1969). Assuming a mixed diet of crustaceans and Arctic cod with a mean energy content of 6.3 MJ/kg (Gjertz & Lydersen 1986; J. M. Weslawski, M. Ryg, T. G. Smith & N. A. Øritsland, unpubl. data), the average daily consumption would be 4.9% of body mass.

Our analysis suggests that the food intake of adult ringed seals varies seasonally; this agrees with the seasonal changes in gastrointestinal contents reported previously (Ryg et al. 1990). Seasonal changes in food intake have been observed in captive harbour seals and grey seals fed ad libitum (Ashwell-Erickson & Elsner 1983; Nordøy & Blix 1988; Renouf et al. 1988). Phocid seals have also shown pronounced seasonal body mass changes which correlate with the reproductive and moulting cycles (Bowen et al. 1987; Fedak & Anderson 1982; Stewart & Lavigne 1984). Such metabolic cycles are common in large animals living in seasonal environments. The cycles tend to persist in captivity; they are probably genetically determined adaptations partly to the seasonal variations in energy requirements during the reproductive cycle and partly to variations in the quality and availability of food (Ryg 1986). Primary production is low underneath the ice; as a consequence, relatively little energy is available to the consumers when the sea is covered with ice and during the first time after ice breakup. Later in the season, the energy that has been captured by the phytoplankton is passed on to crustaceans and fish and is then available to the seals (Falk-Petersen et al. 1990). Therefore the rebuilding of the seals' fat reserves probably coincides with the time when the abundance and energy content of food is the greatest. On the other hand, the loss of body mass among adults in the spring is primarily an adaptation to seasonal breeding and moulting. Attendance to pups or territorial defense leaves less time for feeding, and relying on fat reserves might thus be advantageous.

In many phocid seals the females stop eating during lactation so that the cost of milk production is covered completely by the body energy reserve of the mother. This strategy may not be possible in an animal with such a small body mass as the ringed seal, and continuation of feeding and a relatively long lactation period may be consequences of small body size (Smith et al. 1991). If feeding continues during lactation, as our analysis suggests, pupping areas may not only be limited by ice and snow conditions, but also by food abundance in the area.

The parameters that most influenced the estimates of total annual consumption were those related to activity. More precise estimates of food consumption would therefore require field studies of the activity and behaviour of ringed seals throughout the year.

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