Food energy requirements of the harp seal (*Phoca groenlandica*) population in the Barents and White Seas

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The harp seal (*Phoca groenlandica*) population of the Barents and White Seas has probably decreased from about one million individuals to half this size the last few years. Energy requirements of the population have been estimated by use of the simulation model SEAERG. In this model the energy requirements of an individual seal from each age group is multiplied with the group size and summed to provide the requirements of the population. In addition to population size and age structure the total food and energy requirement is sensitive to individual activity levels as well as metabolic levels and other specified physiological functions. The interactions between the seal population and fisheries depends on the caloric density of the prey species which varies with season and location. Realistic simulations of interactions between seals and fisheries require more information about spatial and temporal variations in the prey selection of harp seals than is available today.

Present estimates indicate average maintenance requirements of about 13,600 and 11,150 kcal/day for adult female and male harp seals respectively. The high value for the females is due to the costs of pregnancy and lactation. With a mean energy density of prey of 1500 kcal/kg, the corresponding food consumption is 9 kg/day for females and 7.4 kg/day for males.

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Introduction

The population size of harp seals (*Phoca groenlandica*) living in the Barents Sea and White Sea areas may have increased by about 5% per year in the late 1970s (Benjaminsen 1979) and was estimated at about one million individuals in 1985.. Photographic surveys carried out by Soviet scientists indicate that the population growth levelled out in the early 1980s and that the number of breeding females drastically decreased from about 140,000 to about 71,000 during 1985–88 (Anon 1988). However, documentation of survey techniques and subsequent data analysis is not available.

Harp seals may eat considerable quantities of fish, including cod (*Gadus morhua*), capelin (*M[illegible]lotus villosus*), herring (*Clupea harengus*) and various crustaceans (Sivertsen 1941), but there is a paucity of information regarding both feeding rates and dietary preferences in relation to prey availability. Recent work indicates that harp seals may be opportunistic feeders (Sergeant 1973; Lavigne et al. 1982; Lydersen et al. 1991; Kapel & Angantyr 1989).

Both the West Ice and the White Sea populations normally feed in the northeast Atlantic, Svalbard-Barents Sea areas (Sivertsen 1941), but invasions of harp seals to eastern Finnmark have been observed in 1901–1903, 1916–1918 and recently in 1978–1988 (Øritsland 1990). The most recent harp seal invasion caused severe damage to the coastal fisheries at Finnmark, due partly to damage to fishing gear and partly to fish disappearing from the area (Øritsland 1990). Besides constituting a potentially severe problem for commercial fisheries, the sheer number and mobility of harp seals make them an interesting object in the context of ecological studies.

The costs and logistic problems involved in carrying out studies of free living harp seals are high. Indirect methods may be used in order to gain knowledge about the ecological role and potential impact of harp seals on fish stocks and commercial fisheries. The present work concerns an application of a physiologically based model for population energetics (Øritsland & Markussen 1990) to evaluate the food requirements of the Northeast Atlantic harp seal stocks. The role of harp seals in the ecosystem and their potential impact on fish stocks are discussed.

Methods

Available information on life history and energetic physiology of harp seals was analysed using the SEAERG model in order to evaluate the annual energy budget of harp seals (Øritsland & Markussen 1990). The model encompasses two major modules. One calculates the total energy requirements and nutritional status, body size and composition of individuals, while the second provides population forecasts according to a Leslie matrix model. The modules are coupled, allowing the energy requirements of the population to be determined by multiplying the individual needs by the size of the corresponding cohort. Speculations or assumptions regarding density-dependent effects are excluded from the present version of the model structure. With exception of death by starvation there is no automatic feedback from energy balance to mortality and reproductive rates in the present version of SEAERG.

The module for energy balance calculations comprises two parts or submodules. One submodule simulates deep body temperature and the second calculates body size composition. Temperature regulation is achieved by means of a controller simulating the central nervous system, i.e. hypothalamic action. Body size and composition are determined by balancing the food energy intake against the energy required for maintenance and growth.

The energy requirements of the population are estimated in three steps. First, the population size and age structure are estimated. Next the energy requirements of individuals are estimated for each age group according to a given energy feed level and time period. Finally, energy requirements are multiplied by the numbers of individuals in each age group, giving an estimate of energy requirements of the population. Input energy is transformed to food mass by dividing energy with the appropriate energy density of each species of prey.

For the present application, SEAERG was modified with respect to the following parameters:

For herring (*Clupea harengus*) as the only prey, the metabolisable energy represents between 86.1 and 89% of the gross energy consumed (Keiver 1984). In contrast only 60.9% of gross energy was realised as metabolisable energy for shrimps (*Pandalus borealis*) alone (Keiver 1984). Since harp seals eat a number of prey species of variable caloric densities, we generally assume that 80% of the gross ingested energy is realised as metabolised energy. The value 60% was used in one case simulating that the seals were eating amphopods (*Parathemisto* sp.) exclusively.

The swimming distance from the White Sea to the feeding grounds is about 2000 km, i.e. 4000 km migration movement per year. A time activity budget allowing for this distance and an additional 20,000 km/year, 65 km/day was used. The day was split into four parts, the corresponding time and activity fractions being 0.25, 0.60, 0.06 and 0.09 and 1.0, 1.8, 4.2 and 8.4 respectively. This implies that 6 hours a day is spent resting, about 14.5 hours swimming slowly at 3.5 km/hr, about 1.5 hour swimming at 7 km/hr and 2 hours at 10.5 km/hr. For the two haul-out periods, birth and moulting, the time activity budget was set to time fractions 0.6 and 0.4 with activity factors 1 and 2.1. The ambient conditions were set to seawater temperature 1°C, air temperature −3°C and wind speed 0.5 m/s.

Body growth was set to follow the curve given by Innes et al. (1981) for both sexes and modified within each year in order to accomodate for mass losses due to pupping, weaning and moulting (Fig. 1). Initial fat content was set to 40% declining to 18% for females during the lactation period. The productive rates used were 0.9 from age 4 years to maximum life age 25 years while mortality rates for both sexes were 0.2, 0.16, 0.13, 0.11 and 0.10 for ages 0, 1, 2, 3, 4 and 5 respectively followed by 0.095 for ages 6–19 and 0.1, 0.12, 0.19 and 0.24 for the consecutive age groups (Bowen 1985). This corresponds to a population growth of 6.4% per year while one alternative assumption that reproduction does not start before females are six years old results in an annual population growth of 3.4%. Considering the uncertain precision in the estimates of the 1985–88 decline of the White Sea population and that the West Ice population partially inhabits the same waters, a population size of one million individuals was used for the present simulations.

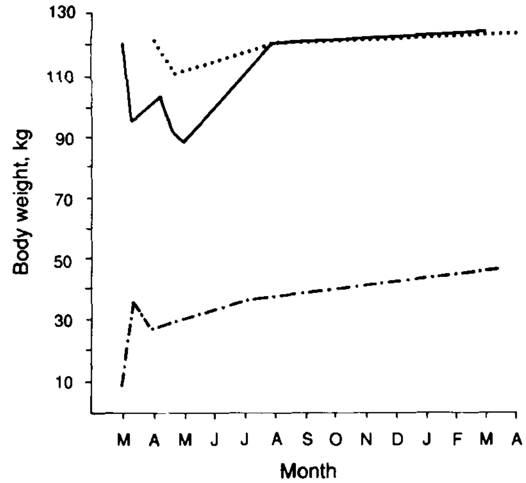

Fig. 1. Monthly total body mass used in the present simulations of the food energy requirements of harp seals. Solid line = adult females; dotted line = adult males; broken line = first year males and females.

Results

From sexual maturity and onwards the energy requirement of the female seals is 13,600 kcal/day, which is about 20% higher than the 11,150 kcal/day for males. The difference is due to the body mass changes associated with birth and lactation.

The energy cost of temperature regulation varies with season due to associated changes in blubber thickness (Fig. 2). Decreasing the air temperatures from −3°C to −10°C caused a 20 to 25% increment of the rate of mass loss for hauled out seals. On the other hand, an increase in water temperature from 1°C to 4°C caused a 7 to 9% reduction of the energy requirement for maintenance.

The observations of harp seals eating predominantly the amphipod *Parathemisto* sp. (Lydersen et al. 1991) while polar cod (*Borogadus saida*) also was available is interesting. The energy density of *Parathemisto* sp. may vary from 810 to 1200 kcal/kg, the low value occurring in May and the high value in July (G. Gabrielsen, Univ. of Tromsø, pers. comm). Using an energy density of 1,000 kcal/kg and 60% as metabolisable energy (Keiver et al. 1984), SEAERG simulations suggest that an average male harp seal of 120 kg would have to eat 22 kg *Parathemisto* sp. daily for maintenance.

The food requirement of the seals depend on the energy content of the prey species and may, under the general assumptions for the present simulations, vary from 1.4 to 4.4 million tonnes per year for one million harp seals (Fig. 3).

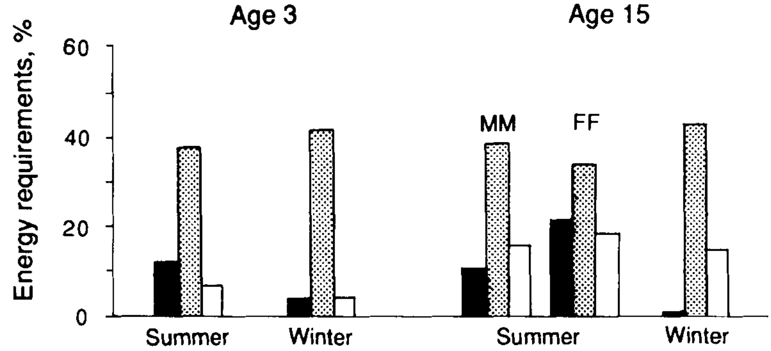

Fig. 2. The relative requirements for growth (solid bars), maintenance (shaded bars) and temperature regulation (open bars) in the total energy budget of resting 3 year-old and 15 year-old harp seals.

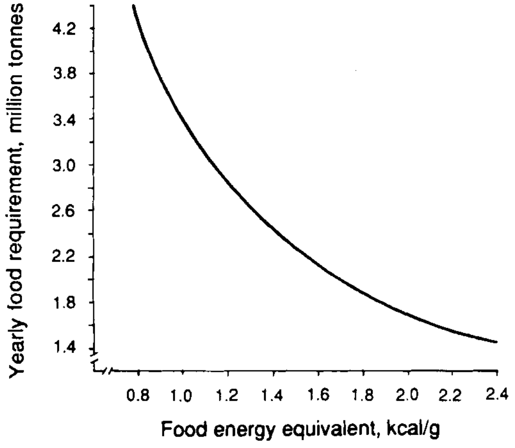

Fig. 3. The food requirements of one million harp seals in relation to the energy density of prey species.

Discussion

The energy requirement of the population is equal to the requirements of the individual multiplied by the corresponding age group size; the population requirement is therefore directly proportional to the age group size. Long term limitations in food supply activate physiological mechanisms that cause significant deviations from the normal relationship between individual and population energy needs (Øritsland & Markussen 1990). However, these are not invoked in the present application.

The present application of SEAERG is comparable to the annual energy budget model developed by Lavigne et al. (1985) for evaluation of the food consumption of the Northwest Atlantic harp seals. The higher estimate found by use of SEAERG may be ameliorated by adjusting the present values for digestibilities, the energy density of the prey species eaten, or time activity budgets.

A major difference between the present model for harp seal energetics and the model presented by Lavigne et al. (1985) is that SEAERG includes several functions for physiological mechanisms that will cause significant density-dependent effects both at the individual and at the population level as the seal's food resources are depleted (Øritsland & Markussen 1990). An interesting effect of these functions is that the estimate of individual energy requirements may change in a manner quite different from that of the population. Therefore considerable care should be taken with respect to transforming from population to individual needs or vice versa when the population size is assumed to approach a K level, or the carrying capacity for the habitat. However, the present application assumes no limitations on food availability.

Harp seals in the Northeast Atlantic appear to spend a major part of their time in areas that are exploited by commercial fisheries. There is no doubt that harp seals eat commercial fish species and that the Northeast Atlantic populations in principle compete with the fisheries. It is not possible, however, to evaluate the impact of local predation on individual fish stocks, mainly because prey selection is poorly known, and also because of differences in terms used by various authors. For example Sergeant (1973) who suggested that fish constituted 60% of the total food intake of which 25% was capelin, reported on frequencies of different food items without reference to volume, mass or energy content. Kapel & Angantyr (1989) reported volume and weight estimates including value for fish represented by otoliths remaining in the stomach. Capelin, polar cod, arctic cod (*Arctogadus glacialis*), redfish (*Sebastes* sp.), sandeel (*Ammodytes* sp.) and euphausiids were reported only in qualitative terms as important food items. Lydersen et al. (1991) excluded trace elements like otoliths and squid beaks and found that amphipods, mainly *Parathemisto libellula* were the most significant food item of harp seals in the northern Barents Sea during August–September. Capelin and polar cod are indicated to be dominant items of harp seals in the Northwest Atlantic (I-H. Ni, Dept. of Fisheries and Oceans, Newfoundland, pers. comm.).

Models such as SEAERG might be used in simulations to investigate the potential impact of harp seals on fish stocks, but can not be used directly in management decisions before more information is collected with respect to both behavioural and physiological characteristics of seals as consumers in the North Atlantic ecological communities. Assuming, for example, that the harp seals in the Barents Sea take herring or capelin (2000 kcal/kg) exclusively, the consumption would be about 1.5 million tonnes per year, three times more than the total herring stock size estimated for these waters for the mid eighties, or between 1/4 and 1/3 of the total capelin stocks older than two years. If cod (1000 kcal/kg) constituted the exclusive diet of the harp seals, the consumption would be 3 million tonnes per year which is three times more than the stock estimate. It should be noted in the same perspective that 77,000 minke whales would have comparable food requirements (Markussen et al., 1992).

The attraction of energetics models such as SEAERG is that they are based on fundamental physical and physiological theory and provide good estimates of food energy needs. Thus, if behavioural links between seal and prey in terms of locomotion and dietary preferences can be established, the role of these seals in the natural mortality of commercial fish stocks may be estimated. The residual error in statistically derived fisheries management models might thus be reduced and the analysis of the effects of other factors such as sea temperature and other abiotic variables improved.

Fisheries may be developed to take more fish than the seals can consume as long as fish stocks are abundant, but fisheries will probably decline for economic reasons when commercial species are depleted. On the other hand the harp seals, because of their agility, their capability to pick out individual fish and shrimp, and the fact that they live in the areas may be able to continue harvesting depleted commercial stocks even when the density is too low to be exploited by fisheries. Simulations of harp seals living on noncommercial crustacean species, such as *Parathemisto* sp. suggest that the seals may need fish in the diet. The requirement for about 22 kg *Parathemisto* sp. per day for an average 120 kg harp seal male may correspond to an intake volume of about 40 l/day. This means processing of large meals, for example 10 l every six hours or 5 l every third hour. It remains to determine whether the digestive system of harp seals has such a capacity and whether the energy cost of collecting such amounts of prey would be excessive. Supplementary feeding on noncommercial fish species might be a prerequisite for the harp seal's possibilities for survial on other prey species.

There are obvious needs for information about swimming speeds, activity patterns and food selection in relation to availability for free ranging seals. It appears difficult, however, to obtain sufficiently precise observations of food selection and prey treatment in the open seas, and analysis of stomach contents will not provide sufficient information regarding food processing rates. McLaren & Smith (1985), reviewing pinniped ecology, suggested that "experimental introduction of harbour seals into well-chosen lakes might tell us more about the role and control of pinnipeds in ecosystems than could the most extensive studies of unbounded seals or the most elaborate models in the largest computers". We concur, on the basis of our computer work, with this suggestion, but would consider a marine area with penned in skerries and sounds a better facility. The advantage of such a facility is that captive seals easily and repeatedly could be offered live fish of predetermined size, while selection and handling could be observed directly from underwater installations. Areas ranging from laboratory size to sizes allowing the seals considerable freedom of movement could be set up by use of underwater fences, and small-scale ecological community relations could be examined experimentally. At the same time the need for continued experimental work in the laboratory is identified by a long array of reports, including our SEAERG developments, and should not be downgraded.

It is necessary to have a wider scope of principles than those encompassed by population dynamics and energetics in order to design ecosystem or multispecies models, but energetics provide constraints that must be met. It is not possible to divine when such models eventually might become useful in practical management, but we are bound to continue expressing current knowledge by use of computer models. The challenge is to strengthen the daily interaction between modelling and practical field and laboratory work.

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