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Food consumption of the NE Atlantic minke whale (*Balaenoptera acutorostrata*) population estimated with a simulation model

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A physiologically-based simulation model was used to estimate the energy requirements and food consumption of the NE Atlantic minke whale population. The parameters used in the model are based on measurements of minke whales caught during the scientific whaling in 1988 and 1989, as well as values from the literature. The average daily energy requirements were 1.9×10^5 kcal for adult females and 1.4×10^5 for adult males. Assuming that minke whales acquire 90% of their yearly energy requirements during the summer, with a diet consisting of 50% crustaceans and 50% fish, the daily food consumption will be 277 kg for adult females and 204 kg for adult males. This implies that NE Atlantic minke whale population, estimated at 77 000, has a total food consumption of about 2.2 million tonnes during a feeding period of 5 months in the NE Atlantic Ocean.

Key words: minke whale, energy, food, model, North Atlantic.

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Introduction

The minke whale (*Balaenoptera acutorostrata*) is abundant in Norwegian waters with a total population estimate in the NE Atlantic of 77 000 (43 500–114 000, 0.95% c.i.) (IWC, 1991). Minke whales have a varied diet compared to other baleen whales which includes economically important fish species such as herring (*Clupea harengus*) and cod (*Gadus morhua*) (Larsen and Kapel, 1981; Jonsgård, 1982; Lydersen *et al.*, 1991). To be able to assess the importance of minke whales as consumers in the marine ecosystem and their impact on fisheries, information is needed about their energy requirements. In the present work a physiologically-based simulation model for population energetics, SEAERG, originally developed for harp seals (*Phoca groenlandica*) (Øritsland and Markussen, 1990), is modified for minke whales to estimate the energy requirements of the NE Atlantic population.

Methods

The simulation model used to estimate the energy requirements of minke whales consists of two coupled modules: one calculates total energy requirements and nutritional status, while the other provides population forecasts according to a Leslie matrix model as described by Øritsland and Schweinsburg (1983). The module for energy balance consists of two submodules; and regulates deep body temperature and calculates body size and composition (fat content, lean body mass) by balancing food energy intake against the energy required for maintenance and production, including growth and reproduction (Fig. 1) (Øritsland, 1977, 1990; Øritsland and Markussen, 1990). Temperature regulation is achieved by means of a controller simulating the central nervous system. The heat loss is calculated by considering the body trunk as a flat double-layered wall and the flippers as flat surfaces (Øritsland, 1974; Øritsland and Ronald, 1978). Since body mass, body composition and surface area are factors influencing the heat balance, we have modified these equations in accordance with measurements from minke whales.

The energy requirements of the population are determined by multiplying individual needs by the size of the corresponding age group. Input energy is transformed to food mass by dividing by the energy density of the prey.

The physiological parameters used in the model are based on measurements of 25 minke whales, as well as values from the literature for both minke whales and other rorquals. In some cases, it has also been necessary to use values measured from seals.

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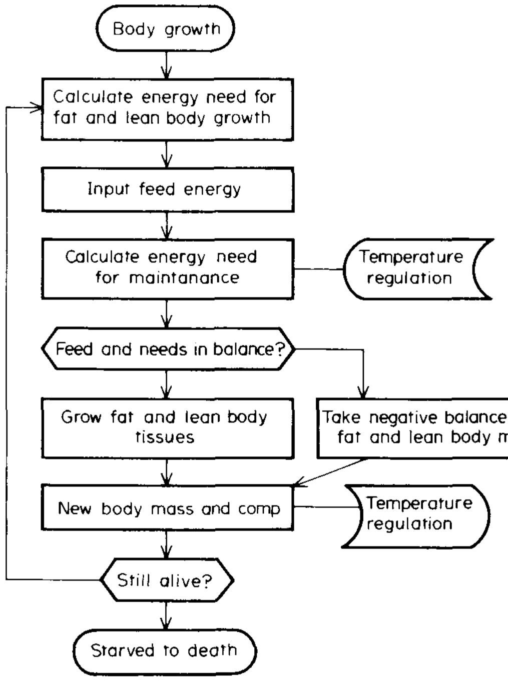

Figure 1. Flow diagram for the SEAERG submodule simulating body growth and composition and integrating input from the submodule for temperature regulation into the complete and age-specific energy budget of individuals (from Øritsland and Markussen, 1990, with permission).

The age was determined from laminated structures in the tympanic bullae (Christensen, 1981).

Collection of data

Data from 25 minke whales killed during scientific whaling in the Lofoten-Vesterålen area (68–69°N, 13–16°E) in August 1988 and west of Svalbard (77–78°N) in July 1989 are used in this study. The total body mass of 18 whales were measured to the nearest 5 kg using a strain gauge load cell with an electronic digital indicator (Toledo 8140) and a weighing net built for this purpose. Three whales were weighed in parts and corrected for fluid loss. Body masses of another four whales were estimated from length and girth data based on the formula

$$W = 46.9 \times \text{Girth}^{1.23} \times \text{Length}^{1.45},$$

(Lockyer and Waters, 1986). Masses estimated from this formula were not significantly different from measured body masses (Fig. 2; paired t-test, $p > 0.2$, $n = 18$). Total lengths and girths for every 0.5 m along the body were measured. The blubber was dissected off and weighed. Flippers and flukes were photographed against a background table with known dimensions and their surface areas measured with a planimeter. The surface area of the

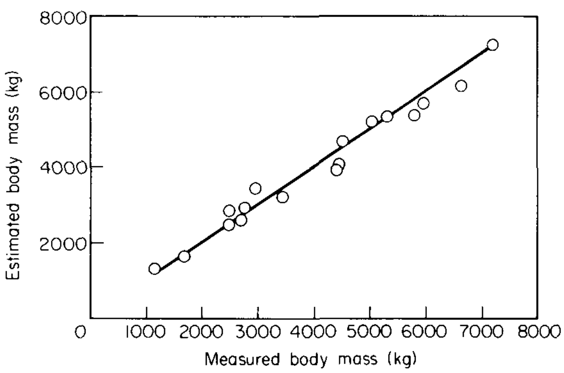

Figure 2. The relationship between estimated body mass from the formula $W = 46.9 \times \text{Girth}^{1.23} \times \text{Length}^{1.45}$ (Lockyer and Waters, 1986) and the measured body mass of 18 minke whales.

body and head was calculated using the measured circumferences and considering the body as a series of truncated cones.

Modifications of the SEAERG model

The seasonal movements of the whales may be connected with intensive feeding in summer and mating and calving in winter, and result in a seasonal variation of the body mass. This variation, however, is not considered in the present simulations as we have assumed 365 identical days. This implies both a similar mass gain and activity pattern every day. The main reason for doing this is that we lack information on mass loss during winter, and it is not known whether minke whales have a metabolic depression during starvation, as shown in seals (Nordøy *et al.*, 1990; Markussen *et al.*, 1992) and in terrestrial mammals during both starvation and restricted food intake (Keys *et al.*, 1950; Markussen and Øritsland, 1986).

Metabolic rate

As the available estimates of metabolic rates in whales are in accordance with those predicted for other mammals under similar conditions (Innes *et al.*, 1986), we have expressed the resting metabolic rate (M) according to Kleiber's equation (Kleiber, 1975):

$$M = 70\,W^{0.75} (\text{kcal day}^{-1}),$$

where W is body mass (kg). However, growing young and sexually immature mammals, both terrestrial and marine, have higher metabolic rates (Wahrenbrock *et al.*, 1974; Kleiber, 1975; Innes *et al.*, 1986). The model incorporates this higher metabolic rate by multiplying with a factor AWF denined as:

$$AWF = \begin{cases} -0.17\,\text{age} + 2.17 & \text{age} < 7 \text{ years} \\ 1 & \text{age} \geq 7 \text{ years} \end{cases}$$

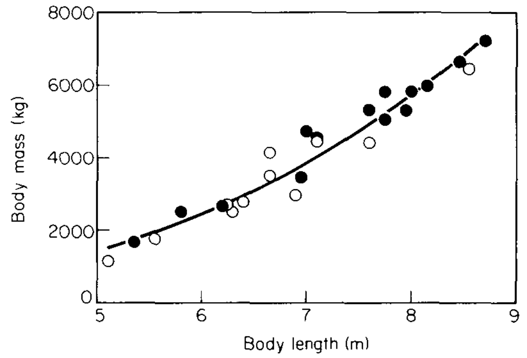

Figure 3. The relationship between body length and body mass in minke whales.

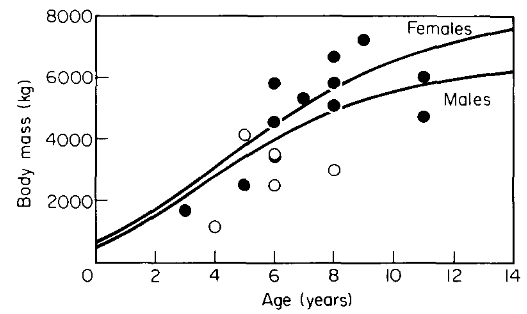

Figure 4. The growth of female minke whales in the north-east Atlantic estimated by a Gompertz curve. Measured body masses: ○ females, ● males.

Body mass–body growth

We used a Gompertz curve (Kaufman, 1981) to approximate the growth of minke whales. Christensen (1981) reported that asymptotic lengths of female and male minke whales in the North Atlantic were 9.07 and 8.33 m, respectively. Using the body mass to length relationship from our material (Fig. 3), this gives asymptotic body masses of 8300 kg and 6500 kg for females and males, respectively. The constants in the equations were adjusted to give body masses of 60% of asymptotic values at sexual maturity, which is 7 years for females and 6 years for males (Christensen, 1981). We have expressed the body mass of minke whales, W (kg), as a function of age (years) by the following growth curves:

females: $W = 8300\,e^{-2.6e^{-0.235\text{age}}}$

males: $W = 6500\,e^{-2.6e^{-0.275\text{age}}}$

(Fig. 4). Seasonal changes in body mass are not incorporated in the model because data are not available.

Blubber content

The blubber constituted $17.0 \pm 1.4\%$ (mean ± S.D.) of total body mass. The percentage of blubber content was not significantly correlated with body mass based on our measurements from minke whales in July and August.

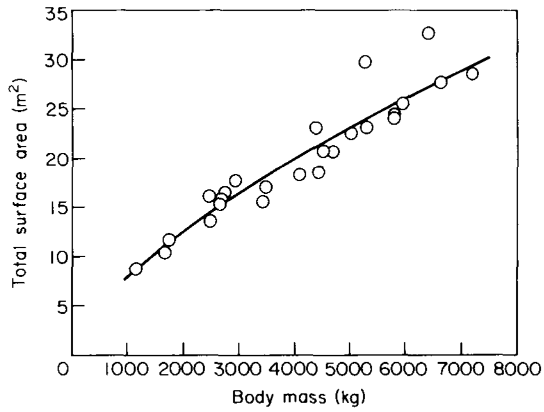

Figure 5. The relationship between total surface area, m², and body mass, kg, in minke whales.

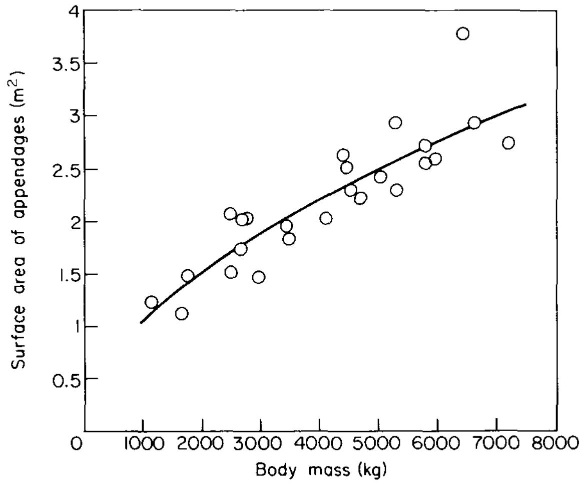

Figure 6. The relationship between surface area of appendages, m², and body mass, kg, in minke whales.

Surface area

The total surface area, AT(m^2), may be expressed as:

$AT = 0.0760\,W^{0.67}$ $\quad r^2 = 0.929$

(Fig. 5) and the area of fins, flippers and flukes, AFF(m^2), as:

$AFF = 0.0235\,W^{0.55}$ $\quad r^2 = 0.816$

(Fig. 6).

Activity

Marine mammal activities include foraging, moving between food patches and migratory movements to other areas. During migration speeds up to 7.2 m s^{-1} have been observed in minke whales (Lockyer, 1981), while their normal swimming speed is about 1.7 m s^{-1} (Williamson, 1972; Lockyer, 1981).

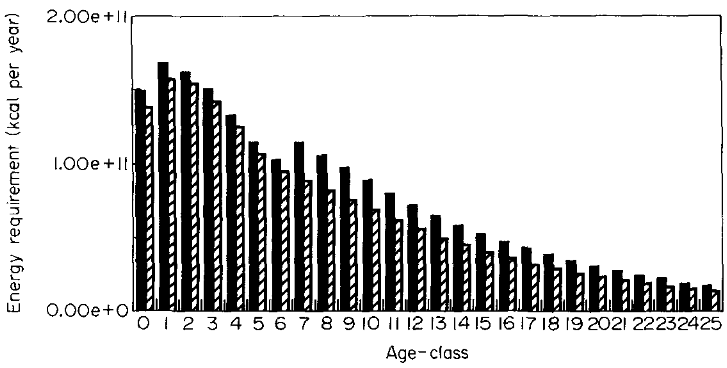

Figure 7. The total annual energy requirement, kcal, for each age-class and sex in minke whales (■ female, ▨ male).

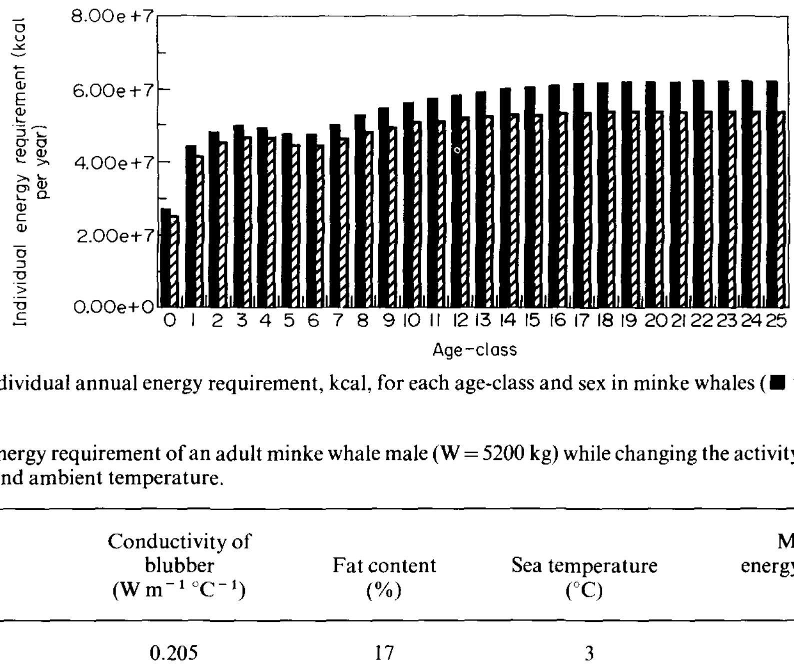

Figure 8. The individual annual energy requirement, kcal, for each age-class and sex in minke whales (■ female, ▨ male).

Table 1. Changes in energy requirement of an adult minke whale male (W = 5200 kg) while changing the activity level, conductivity of blubber, fat content and ambient temperature.

Mean daily swimming distance (km day^{-1})	Conductivity of blubber ($W m^{-1} °C^{-1}$)	Fat content (%)	Sea temperature (°C)	Mean daily energy requirement (kcal)
188	0.205	17	3	133 500
98	0.205	17	3	109 400
248	0.205	17	3	150 000
188	0.186[1]	17	3	125 900
188	0.290[2]	17	3	167 900
188	0.205	12	3	163 800
188	0.205	17	10	110 300

[1]From Scholander *et al.* (1950).
[2]From Hart and Irving (1959).

In the activity budget the day was split into three parts, allowing for sleeping, resting and swimming in accordance with observations from whale hunters and from following a radio-marked minke whale (Øen, 1990). As a mean, 6 h a day is spent resting and sleeping, 14 h swimming at a speed of 1.7 m s^{-1}, with an assumed increase of the metabolic rate of 20% (activity factor = 1.2), and 4 h a day is spent at their migration speed of 7.2 m s^{-1}, with an assumed tripling of metabolic rate (activity factor = 3).

Reproduction

In addition to the energy requirements for maintenance and growth, mature females need energy for pregnancy and lactation. During the gestation period the foetus grows to a mass of 280 kg, estimated from the length as newborn (Christensen, 1981), with an average energy density of 2350 kcal kg^{-1} (Lockyer, 1981). This corresponds to a maternal energy investment of 0.7×10^5 kcal. Concurrent with this investment, the female must expend energy to maintain the growing foetus. This cost is expressed as the heat increment of gestation and is estimated based on two relations described by Robbins (1983) to be 2.3×10^6 kcal.

The lactation period lasts about 4 months. The energy in milk must cover the sum of production of calf tissue and the maintenance requirements of the calf. The calf is assumed to grow at a rate of 5 kg per day. The maintenance requirements of the calf are calculated in the same way as that of other juveniles. This results in a daily milk production of 11.9 kg, with a caloric content of milk of 4140 kcal kg^{-1} (Lockyer, 1981). The total cost over the entire lactation period is 8.4×10^6 kcal.

This results in a total maternal investment of about 11.5×10^6 kcal in foetal growth, heat of gestation and the cost of lactation.

Metabolizable energy

Stomach content analyses show much variation in the diet of minke whales (Larsen and Kapel, 1981; Jonsgård, 1982; Lydersen *et al.*, 1991). The energy content of the diet varies from 900 kcal kg^{-1} when feeding on *Parathemisto* spp. to as high as 3000 kcal kg^{-1} when feeding on herring. In seals, metabolizable energy varies from 60.9% of gross energy intake eating shrimps (*Pandalus borealis*) to 88% eating herring (Keiver, 1982). Composition and energy content of the diet will vary both seasonally and annually but usually consists of a mixture of fish and crustaceans; we have therefore set the metabolizable energy to 80% of the gross energy intake in our simulations.

Population size and parameters

Surveys in 1988 and 1989 have resulted in an estimate of 77 000 minke whales in the NE Atlantic (IWC, 1991). In our simulations we have used this population size and assumed a stable age structure, a sex ratio of 1:1 and an annual mortality of 10% for all age classes except the first where the mortality is set to 30%. The age of sexual maturity in females is set to 7 years (Christensen, 1981) and the pregnancy rate 78.4% (Best, 1982), equal to birth rate.

Results and discussion

The total annual energy requirements for each age-class range between 1.26×10^{10} and 16.8×10^{10} kcal (Fig. 7), resulting in an estimate of the total annual energy requirements for the NE Atlantic minke whale population of 3.7×10^{12} kcal, or a consumption of about 2.5 million tonnes food with an energy density of 1500 kcal kg^{-1}. The individual annual energy requirement ranges between 2.7×10^7 and 7.4×10^7 kcal in females and between 2.5×10^7 and 5.4×10^7 kcal in males according to age (Fig. 8), the average daily energy requirement being 1.9×10^5 kcal for adult females and 1.4×10^5 kcal for adult males. If minke whales were to cover their annual energy requirements by eating the same amount every day throughout the year, the population of 77 000 individuals would need 1.5×10^{12} kcal during their 5 months in the NE Atlantic. If minke whales, however, have their feeding period in the NE Atlantic and like fin whales (*Balaenoptera physalus*) acquire 90% of their total energy requirements for the year during this period of about 5 months (Lockyer, 1986), the minke whale population would need a total of 3.4×10^{12} kcal during the 5 months that they spend in NE Atlantic.

The energy requirements are sensitive to the parameter values used in the model (Table 1). Changing the heat conductivity of blubber from 0.205 W m^{-1} °C^{-1} (Parry, 1949; Carlson and Hsieh, 1970) to 0.29 W m^{-1} °C^{-1} as estimated in live seals (Hart and Irving, 1959) increases the energy requirements by 26%. On the other hand, changing the conductivity of blubber to 0.186 W m^{-1} °C^{-1} as estimated in dead seal blubber (Scholander *et al.*, 1950), results in a decrease of the energy requirement by 6%. The blubber content used in our simulations is based on measurements from minke whales in July and August. Measurements in other periods of the year may give lower blubber content resulting in poorer insulation and hence a higher energy requirement. Decreasing the blubber content from 17 to 12%, for example, increases the energy requirement by 22%. As rorquals migrate to higher and colder latitudes in summer and lower and warmer latitudes in winter (Lockyer, 1987), their ambient temperature changes throughout the year. The energy requirement also depends on the water temperature; increasing when the temperature is low and decreasing when the temperature is high.

The activity level also influence the energy requirement estimates (Table 1). Decreasing the mean daily swimming distance from 188 km to 98 km results in an 18% decrease in the daily energy requirement. Conversely, increasing the mean daily swimming distance to 248 km results in a 12% increase in the daily energy requirement. The measured body masses were higher in males and lower in females than estimated from the growth curves (Fig. 4). Nevertheless, we have used the expressed body masses from the growth curves to estimate the energy requirements.

The mass of food required depends on its energy content. Most of the stomachs analysed had a mixture of crustaceans and fish (Larsen and Kapel, 1981; Jonsgård, 1982), while Lydersen *et al.* (1991) found mostly herring in the stomachs of 15 minke whales taken in the Lofoten-Vesterålen area. Depending on the composition of the diet and how much they eat in the different seasons, the daily food consumption ranges between 63 and 462 kg in adult females and 47 and 340 kg in adult males. Assuming that mink whales acquire 90% of their energy requirement during summertime and a diet consisting of 50% crustaceans and 50% fish (1500 kcal kg^{-1}), the daily food consumption in an adult minke whale will be 277 kg in females and 204 kg in males, which is in agreement with results reported by others (Sergeant, 1963; Lockyer, 1981; Innes *et al.*, 1986). This results in an estimated food requirement of about 2.2 million tonnes of a 50:50 fish/crustacean diet for a minke whale population of 77 000 during a feeding period of 5 months.

There is no doubt therefore that the amounts of fish eaten by minke whales are such that it would clearly be desirable from a fisheries assessment point of view to take into account the interactions between whales and fish. Assuming, for example, that the fish in the diet consists of 20% herring, 10% capelin, 10% cod and 10% other fishes, such a diet implies a consumption of 440 000 tonnes of herring, which is more than five times the commercial herring catch during 1990; 220 000 tonnes of capelin, which is half of the catch in the winter 1991; and 220 000 tonnes of cod, which is of a similar magnitude to the 1990 catch. However, the limited information on local movements and food selection of the whales leaves open the possibility that species of less commercial value might constitute an important part of the energy budget.

The present results give a general indication of how much energy is needed for maintenance and growth for the NE Atlantic minke whale population. Until more is learnt about the activity budget of the whales, their geographical distribution throughout the year and the food composition of the diet, estimates of food requirements and evaluations of their ecological role and possible interaction with the fisheries, remain incomplete.

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