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Density-Dependent Condition and Energetics of Marine Mammal  
Populations in Multispecies Fisheries Management

by

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ABSTRACT

Oxygen consumption of five fasting grey seal (*Halichoerus grypus*) pups was observed over a five-week period. Measurements indicated an orderly sequence of tissue consumption over this period. Blubber is consumed to a heat loss threshold level above which there is a nonlinear increase in resting metabolism. Compensatory bioenergetic strategies are considered relative to individual seals within an expanding population. We conclude that, contrary to some published estimates, nonlinear increase in per capita food consumption is possible with increasing populations of marine mammals, a prospect to consider in any multispecies approach to fisheries management.

INTRODUCTION

Seals, seabirds, and whales are significant consumers of marine production, often in direct competition with fishes and fishermen. Bioenergetic analysis of multispecies fisheries requires realistic appraisal of the energy requirements of all major consumers within the production system. In particular, we need to understand how energy requirements change in response to dynamical variation of demographic parameters.

Changes in body condition and thermal balance provide important criteria of bioenergetic variation for homeotherms such as seals, because these are reflected in a cumulative effect upon the energy consumption of a stock. Estimates of the so-called 'surplus' potential of fish species for commercial harvest can depend to a major degree on the energy consumption of competing mammalian predators, and multispecies management procedures must therefore allow for varying demands for prey organisms as the stocks of predatory mammals themselves vary. Clearly, the bioenergetic requirements of mammalian stocks are important considerations for multispecies approaches to fisheries management (Brodie 1975, 1977; Laws 1977; Gaskin 1978; May et al. 1979).

Two major stocks of marine mammals are now increasing in the North Atlantic. These are the grey seals (*Halichoerus grypus*) of the western North Atlantic (Summers et al. 1978; Gray and Beck 1979), and the harp seals (*Pagophilus groenlandicus*) of the Gulf of St. Lawrence (Lett and Benjaminsen 1977).

There have been attempts to assess the impact upon the food base of the increase in harp seals.

Winters (1975) implied that a 131% change in abundance from  $1.3 \times 10^6$  to  $3.0 \times 10^6$  individuals would result in a 43% increase in food consumption. This view is supported by Innes *et al.* (1979), who concluded that with increasing stock size in harp seals the per capita consumption of energy would be reduced. In effect, these authors conclude that increased intraspecific competition has no detrimental effect upon harp seal condition nor, therefore, upon individual energy requirements; in fact, they infer some aggregate efficiency improvement, on a per capita basis, of energy utilization for growth, maintenance, reproduction, and foraging.

In the present study we have attempted to quantify the change in energy demand with diminishing grey seal condition, measured as a reduction in blubber thickness, and we consider the implications of this change for energy demands by seal stocks in general.

#### MATERIALS AND METHODS

Grey seal pups were used in the study. Five pups, ranging from one to three weeks in age, were captured on the small islands off the west coast of Norway in early November 1977. These were transported to the University of Oslo and held in outdoor tanks. No food was given to the pups during the five-week experimental period. The pups were unrestrained in the outdoor area, being able to choose among three pools which were surrounded by resting platforms. Outdoor air temperature during this period ranged from +10°C to -2°C, and pool water temperature ranged from +8°C to +5°C.

At weekly intervals each seal was placed in a specially designed metabolic measurement chamber in which it was immersed with only the head exposed (water temperature  $7^\circ\text{C} \pm 1^\circ$ ). The seal pups were not otherwise restrained, and  $\text{O}_2$  consumption measurements were taken only when they were observed to be inactive. At the end of each weekly trial, the seals were weighed, and sternal blubber thickness measured using ultrasonic techniques (Kretz Technik, Impulse/Echogerat, #24ME within 10% accuracy  $\pm 0.25$  cm). The results (Fig. 1) are plotted as mean values  $\pm$  standard error. 'Students' t-test was used to determine significant differences between means.

#### RESULTS

There were initial differences in blubber thicknesses among the five animals used in this study, therefore each point in Fig. 1 does not always represent five animals. The trend to increased  $\text{O}_2$  consumption with decreased blubber thickness was demonstrated by following individuals through a period of blubber reduction and, as shown in the figure, was further demonstrated by the cumulative data.

Reduction in blubber thickness from 3 to 2 cm caused no significant change in resting  $\text{O}_2$  consumption. However, a further reduction from 2 to 1.5 cm of blubber thickness resulted in a significant increase ( $P < 0.025$ ) in resting metabolism (of the order of 40% increase in  $\text{O}_2$  consumption).

During the five-week experimental period there were notable changes in behaviour. One change, which could be interpreted as a response to heat loss, was that, as an apparent threshold in heat loss or blubber thickness was reached, the seals hauled out on the platform. Such a change in behaviour would reduce heat loss. There was a sequence in this response, with the most emaciated pups hauling out first. Similar behaviour was observed of common seal (*Phoca vitulina*) retained in open system sea water at Bedford Institute in 1971 (unpub. obs. P.F.B.).

#### DISCUSSION

It is apparent from this study that decrease beyond a critical blubber thickness results in a non-linear increase in metabolic rate. These observations agree with the Irving and Hart (1957) experiments on *Phoca vitulina*. These authors found that a "stunted and skinny" seal had a resting metabolic rate 50% greater at 20°C than another of the same age but superior fat thickness.

The observed reduction in blubber thickness during starvation is consistent with the findings of Sivertsen (1941) and Chapskii (1964). Øritsland *et al.* (in preparation), studying metabolic rates of grey seals, found for one individual with blubber thickness of 3.5 cm that assuming a caloric equivalent of  $7200 \text{ kcal kg}^{-1}$  produced an acceptable simulation of the observed weight loss; but for an animal with blubber thickness of 1.9 cm, the caloric equivalent had to be only  $3900 \text{ kcal kg}^{-1}$ . From the higher caloric values indicated for thick blubber, it would appear that at the initial stage of blubber reduction, lipids are a major source of energy. But once blubber is reduced below some critical thickness, it appears that the thermo-regulatory needs of seals require that fat be conserved. In order to provide an alternate

source of energy, a shift to utilization of body core tissue, primarily protein, is indicated by the reduced energy density that was observed.

Initial consumption of blubber was considered the first response in a feeding reduction experiment by Bigg *et al.* (1978). Similarly, Pernia *et al.* (1979) found fat consumption was an initial priority for fasting northern elephant seals. It is anomalous that the studies of Stewart and Lavigne (1979) on harp seals did not find this to be the case. They found no significant change in fat thickness with starvation, but a 35% reduction in body core weight. To them, this implied that there was no fat consumption indicated and that muscle was consumed in the initial phases of starvation. Estimation of energy storage or consumption rate by measuring body core weight (Stewart and Lavigne 1979), rather than caloric content, may be confounded with changes in water content and fat protein composition, as demonstrated by Bintz *et al.* (1979).

Based on the above findings, we posit the following sequence of tissue utilization during a starvation period: (1) utilization of fat nodules, if present around internal organs; (2) utilization of a portion of the insulative blubber to a critical minimum thickness; (3) utilization, in part, of the muscle core; and as a final resort, (4) utilization of the remaining blubber layer. (A seal in such a critical state would presumably not consume its propulsive tissue to the point of eliminating its effectiveness as a predator, but at some point it would shift back to utilizing its remaining blubber insulation.) In fasting, some muscle is consumed to provide glucose (Brodie 1975).

When we apply our findings to an expanding seal population we find them inconsistent with the conclusions of Winters (1975) and Innes *et al.* (1979). We take this view for the following reasons. An increasing seal stock must at some level of abundance encounter a reduced per capita availability of prey, due to increased intraspecific competition. In consequence, either blubber reserves should decrease, on average, due to lower food intake; or if blubber thickness is maintained, foraging costs must increase. As we have shown (Fig. 1), decreasing blubber reserves below a certain threshold further exacerbate energy requirements because of the increased cost of thermoregulation. Taken together, we view these factors as arguing for a proportionately greater energy requirement by large, increasing seal herds; certainly we find no grounds for the view that large herds could exhibit proportionately greater energy efficiency, once beyond some initial levels of increased abundance.

Detailed appraisals of seal energy budgets are, of course, complicated by many associated considerations, and quantification is correspondingly difficult. It is useful to consider two major avenues of bioenergetic response open to seals encountering increased intraspecific competition for prey resources.

#### Foraging Effort

There are differences in migratory and feeding behaviours among seal species; for example, solitary feeding by grey seals, as opposed to the schooling or formation swimming behaviour observed of migrating and feeding harp seals. With the latter, an increase in stock size could result in an increase in the number of groups rather than in seal numbers within individual groups. Differences such as these should affect the spatial characteristics of a stock's interaction with its prey resource, modifying the stock abundances at which individuals experience the relative effects of competition for food.

Similar consequences could follow from changes in migratory behaviour (Sergeant 1973; Bowen and Sergeant 1979). The question is whether increased seal abundance can be offset by restricted migration, in part at least, by feeding on local prey rather than making extensive migrations to areas of seasonal high production. But migratory patterns have presumably evolved optimally, with selection for areas of maximum prey availability (Sergeant 1973; Jangaard 1974; Schul'man 1974; Brodie 1977), and it is difficult to conceive that changed migratory patterns could often provide increased foraging efficiency for a stock. Accordingly, we find no reason to believe that changed spatial utilization of available prey could in general sustain increased foraging efficiencies in the face of enhanced resource competition.

#### Thermal Maintenance

Of all aspects of the marine mammal energy budget, the costs of thermoneutrality seem the highest, with the possible exception of the lactation period (Lockyer 1978). With an increase in a marine mammal stock there is essentially that much more mammalian surface area exposed to a cold marine environment. In the case of the harp seal, an increase of 131% in stock size (Winters 1975; Innes *et al.* 1979) would mean that the total surface area would be more than doubled. This estimate is conservative, since a large stock would tend to accumulate larger, older animals. Hauling out, as observed in the laboratory experiments discussed above, represents a possible, compensatory behaviour, but this is at best a short term solution to thermal maintenance. Furthermore, with an increasing stock size there would eventually be a higher frequency of individuals approaching critical insulation quality levels, based on our findings. But even where blubber thickness is maintained beyond the critical threshold for thermoregulatory efficiency, this

will not reflect the increased foraging effort and associated energy consumption required to maintain adequate blubber reserves.

Finally, we should remember that the aforementioned increases in harp seal stocks will take place in the face of intensive competition by the commercial fisheries for similar prey (Brodie 1977), further exacerbating the effects of intraspecific competition. In general, therefore, we question the hypothesis that per capita consumption of energy decreases with an increasing stock of marine homeotherms. We suggest that there are sufficient grounds to reach the opposite conclusion. In the context of multispecies management, consideration should be given to the possibility that there is a nonlinear increase in both individual and aggregate energy utilization as stock abundance increases. This is a major potential effect that should not be overlooked in the multispecies management context.

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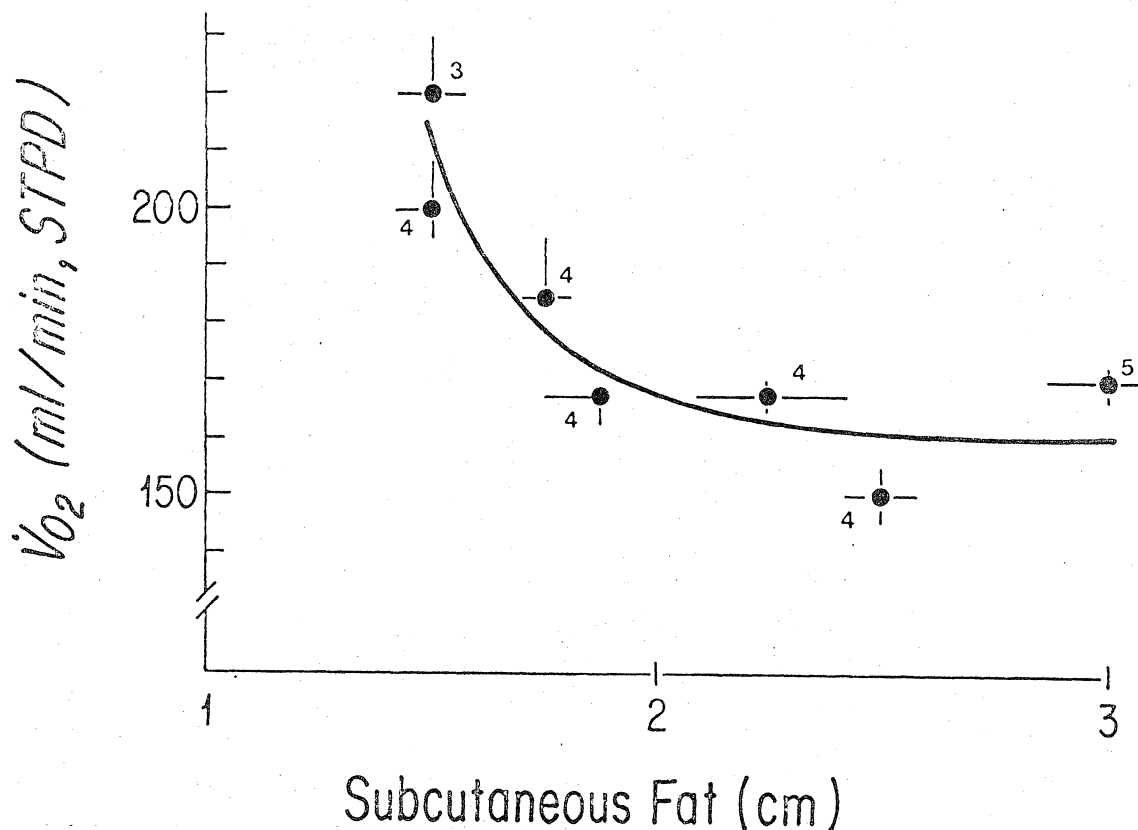


Fig. 1. Resting  $\dot{V}O_2$  consumption in grey seal pups versus subcutaneous fat thickness during a five-week starvation period. Mean values  $\pm$  standard errors are based on five animals with the number representing each point indicated on the graph.