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THE ENERGY COST OF FREE EXISTENCE FOR BERING SEA HARBOR
AND SPOTTED SEALS

University of Alaska

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THE ENERGY COST OF FREE EXISTENCE FOR BERING SEA
HARBOR AND SPOTTED SEALS

A
THESIS

Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
for the Degree of

Doctor of Philosophy

By
Susan M. Ashwell-Erickson, B.A., B.S.

Fairbanks, Alaska

September 1981

THE ENERGY COST OF FREE EXISTENCE FOR BERING SEA
HARBOR AND SPOTTED SEALS

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ABSTRACT

Energy-flow models were developed to assess the net and gross energy requirements of natural populations of Bering Sea harbor seals (*Phoca vitulina richardsi*) and spotted seals (*Phoca largha*), and to estimate their impact on two commercially-important fishes, walleye pollock (*Theragra chaloogramma*) and Pacific herring (*Clupea harengus pallasi*). Energy requirements were estimated from long-term studies of food consumption and proximate composition, food energy content and digestibility, and metabolic effects of temperature, feeding, activity, molt, and reproduction in captive representatives of each species.

Captive seals adjusted their *ad libitum* intake of food to maintain caloric equivalence between diets of varying fat content. The mean digestible energy of pollock and herring was $96.7 \pm 0.2\%$ and $91.2 \pm 0.7\%$ of gross ingested energy, respectively, and the estimated net energy available from both diets was 80.3% of gross energy.

Basal metabolism of both seal species remained constant with season and declined with age. Maximal metabolic effort in water was achieved with harbor seals carrying an 8-kg weight load at an oxygen consumption rate of 32.8 ± 2.8 ml O_2 /kg·min, or approximately four times basal rate. Metabolism during molt in harbor seals was about 10% less than pre-molt levels, accompanied by a rise in plasma cortisol and decline in plasma thyroxine. Reproductive energy costs were estimated at 2.4×10^5 and 2.2×10^5 kcal for individual harbor and spotted seals, respectively.

The annual gross energy required by both populations combined was estimated at 5.6×10^{11} kcal, corresponding to an annual consumption of

8.16×10^4 metric tons of pollock, 5.17×10^4 metric tons of capelin (*Mallotus villosus*), 3.73×10^4 metric tons of herring, and 4.61×10^4 metric tons of invertebrate species, four important prey of these seals. These results suggest that the annual pollock and herring intake of both populations may be about 9% and 20%, respectively, of the present commercial take of these fishes.

TABLE OF CONTENTS

ABSTRACT.	iii
LIST OF FIGURES	viii
LIST OF TABLES.	x
ACKNOWLEDGMENTS.	xii
DEDICATION.	xvi
CHAPTER I --GENERAL INTRODUCTION.	1
The Setting.	1
Pinniped and Fishery Interactions in the Bering Sea.	3
The Framework of Pinniped Energetics.	6
Measures of Energy Expenditure.	8
Estimates of Free Existence Metabolism.	12
Ecological Efficiency in Pinnipeds.	14
Estimating the Energy Cost of Living for Bering Sea Harbor and Spotted Seals	17
The Species	18
The Problem	22
CHAPTER II --ENERGY ASSIMILATION: PROXIMATE COMPOSITION, GROSS ENERGY, AND CONSUMPTION OF FOOD	24
Introduction	25
Methods and Materials.	36
Proximate Composition and Gross Energy of Food.	36
Food Consumption and Body Weight of Captive Seals	39
Results and Discussion	41
Summary.	45
CHAPTER III --ENERGY ASSIMILATION: APPARENT DIGESTIBLE ENERGY OF FOOD.	49
Introduction	50
Methods and Materials.	55
Results and Discussion	59
Summary.	66
CHAPTER IV --ENERGY ASSIMILATION: METABOLIZABLE ENERGY AND SPECIFIC DYNAMIC ACTION OF FOOD	67
Introduction	68
Methods and Materials.	70
Nitrogen Balance Studies.	70
SDA Determinations.	73
Results and Discussion	79
Summary.	86

TABLE OF CONTENTS

(Continued)

CHAPTER V --ENERGY UTILIZATION: ESTIMATION OF NET ENERGY FOR MAINTENANCE.	88
Introduction.	89
Resting and Basal Metabolism	89
Exercise Metabolism.	94
Diving Metabolism.	95
Sleeping Metabolism.	97
Thermoregulation	101
Methods and Materials	105
Metabolism Experiments	105
Exercise Experiments	108
Results and Discussion.	113
Resting Metabolism in Air and in Water	113
Metabolism During Sleep and Normal Activity.	118
Metabolism During Maximal Muscular Exercise.	123
Summary	126
CHAPTER VI --ENERGY UTILIZATION: ESTIMATION OF NET ENERGY FOR PRODUCTION	128
Introduction.	129
Postnatal Growth	129
Body Fat	135
Molt	138
Pregnancy and Lactation.	142
Methods and Materials	146
Postnatal Growth and Body Fat Determinations	146
Metabolic and Hormonal Measurements During Molt.	148
Determination of Reproductive Energy Expenditure	149
Results and Discussion.	150
Postnatal Growth and Accumulation of Body Fat.	150
Metabolic and Hormonal Effects of Molt	155
Reproductive Energy Expenditure.	157
Summary	157
CHAPTER VII --EXTRAPOLATION TO THE NATURAL POPULATION.	160
Introduction.	161
Methods and Materials	162
Results and Discussion.	169
Summary	176
CHAPTER VIII--GENERAL SUMMARY.	178
Proximate Composition, Gross Energy, and Consumption of Food	178

TABLE OF CONTENTS

(Continued)

Digestible Energy.	179
Nitrogen-Corrected Metabolizable Energy.	180
Specific Dynamic Action and Net Energy	180
Net Energy for Maintenance	181
Net Energy for Production.	181
The Energy Cost of Free Existence for Bering Sea Harbor and Spotted Seals	183
BIBLIOGRAPHY.	184

LIST OF FIGURES

FIGURE 1.	Distribution of breeding populations of harbor seals and spotted seals in the North Pacific (after Shaughnessy and Fay, 1977).	19
FIGURE 2.	A simplified budget of energy utilization in an individual non-ruminant mammal (adapted from Harris, 1966; Moen, 1973; Kleiber, 1975)	23
FIGURE 3.	Variation in food consumption with time for one pup (Δ) harbor seal, one yearling (\bullet) spotted seal, and one subadult (\circ) harbor seal	43
FIGURE 4.	Variation of total body weight with time for one pup harbor seal, one yearling spotted seal, and one subadult harbor seal	44
FIGURE 5.	Mean annual food consumption of two spotted seals from ages 1-9 years.	46
FIGURE 6.	Mean annual body weights of two spotted seals from ages 1-9 years. Initial body weights at age 4 months also are indicated	47
FIGURE 7.	Pattern of fecal ^{51}Cr excretion of one yearling harbor seal fed a maintenance ration of herring daily for 8 days	60
FIGURE 8.	Pattern of fecal ^{51}Cr excretion of one 4-year-old harbor seal fed a maintenance ration of herring daily for 8 days	61
FIGURE 9.	Pattern of fecal ^{51}Cr excretion of one 4-year-old harbor seal fed a maintenance ration of pollock daily for 7 days	62
FIGURE 10.	Open-flow respirometry system used in metabolic tests with harbor and spotted seals.	74
FIGURE 11.	Record tracing obtained for sleeping (0-30 minutes) and resting (30-50 minutes) seal during measurement of oxygen consumption with open-flow respirometry	77
FIGURE 12.	The effect of food quantity (herring) and sleep on the magnitude and duration of postprandial metabolic rate in four yearling harbor seals	83

LIST OF FIGURES

(Continued)

FIGURE 13.	Cylindrical exercise tank used in combination with openflow respirometry for measurement of maximal oxygen consumption in seals.	110
FIGURE 14.	Young harbor seal wearing weighted jacket preparatory to treading exercise in cylindrical tank.	111
FIGURE 15.	Variation of mean basal metabolic rate with age for Bering Sea harbor and spotted seals, with data for an Atlantic harbor seal (<i>Phoca vitulina concolor</i>) added for comparison. Curve fitted by eye.	117
FIGURE 16.	Mean basal metabolic rate (kcal/day) of harbor and spotted seals in relation to body weight and to the Kleiber equation $M = 70w^{3/4}$	119
FIGURE 17.	Record tracing of oxygen consumption (heavy line) and carbon dioxide production (light line) of a seal sleeping in water, measured by open-flow respirometry	121
FIGURE 18.	Oxygen consumption <i>versus</i> work load in water for three thermoneutral young harbor seals treading water in an exercise tank.	124
FIGURE 19.	Postnatal growth (weight/age) of harbor seals from the Aleutian Ridge and Pribilof Islands, Alaska. M = maximum weight	151
FIGURE 20.	Postnatal growth (weight/age) of spotted seals from data on captive and wild individuals. M = maximum weight.	152
FIGURE 21.	Variation of total body mass (TEM), lean body mass (LBM), and body fat (FAT) with time for one harbor and one spotted seal	154
FIGURE 22.	Variations in basal metabolism, plasma thyroxine, and plasma cortisol for three yearling harbor seals during the shedding phase of the molt	156

LIST OF TABLES

TABLE 1.	Levels of metabolism commonly reported in the literature (adapted from Gessaman, 1973 and Bartholomew, 1977).	10
TABLE 2.	Values of ecological efficiency (production/ingestion x 100) for species from various trophic levels (adapted from Lavigne <i>et al.</i> , 1977).	15
TABLE 3.	Average composition of typical fatty, semi-fatty, and lean fishes (after Jacquot, 1961)	26
TABLE 4.	Important prey of harbor and spotted seals listed in order of decreasing occurrence. N = total number of seals examined; (n) = number of seals with food present in gut	29
TABLE 5.	Proximate composition and energy content of whole pollock and herring fed to captive harbor and spotted seals.	42
TABLE 6.	The apparent digestibility of different diets in several species of marine and terrestrial mammals	53
TABLE 7.	Apparent digestibility of herring and pollock diets for three species of pinnipeds.	64
TABLE 8.	Food transit time, clearance rate, and gastrointestinal turnover time measured in captive pinnipeds	65
TABLE 9.	Mean daily production and energy content of feces and urine from harbor seals fed maintenance levels of herring and pollock	80
TABLE 10.	Results of nitrogen balance studies conducted over a 5-day period in two age classes of harbor seals fed maintenance rations of herring and pollock. Values in parentheses are calculated from feces output estimated during $^{51}\text{CrCl}_3$ digestibility trials. Values expressed as \bar{x}	82
TABLE 11.	Estimates of energy budget components FE (fecal energy), UE (urinary energy), ME (metabolizable energy), ME_N (nitrogen-corrected metabolizable energy), SDA^N (specific dynamic action), and NE (net energy) for pinnipeds fed herring and pollock	85

LIST OF TABLES

(Continued)

TABLE 12.	Resting metabolic rates measured in 13 species of pinnipeds.	91
TABLE 13.	Metabolic rate associated with diving in pinnipeds	98
TABLE 14.	Metabolic rate associated with sleeping in pinnipeds	100
TABLE 15.	Metabolic tests in air and in water on five age classes of harbor (H) and spotted (S) seals	106
TABLE 16.	Rectal temperatures of harbor (H) and spotted (S) seals before and after metabolic tests in air and in water.	115
TABLE 17.	Sleeping and activity metabolism expressed as multiples of the basal metabolic rate (BMR) in several age groups of harbor and spotted seals.	120
TABLE 18.	Relation of standard to maximal oxygen consumption in several mammals.	125
TABLE 19.	Basic assumptions and prediction equations for Energy Flow Models I and II	163
TABLE 20.	Estimated daily activity patterns and net cost of activity for Bering Sea harbor and spotted seals in relation to molt, reproduction, and other periods. B = birth, W = weaning.	167
TABLE 21.	Energy flow table for a population of 1000 Bering Sea harbor seals	170
TABLE 22.	Energy flow table for a population of 1000 Bering Sea spotted seals.	171
TABLE 23.	Estimated percent of total gross energy required and proximate composition of four important prey in the diets of Bering Sea harbor and spotted seals. S = spring and summer; W = fall and winter.	173
TABLE 24.	Estimated seasonal gross energy requirements and intake of four important prey by Bering Sea harbor and spotted seals. S = spring and summer; W = fall and winter.	174

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DEDICATION

To my late grandmother, Agnes V. Lawlor, whose unwavering faith in my ability inspired me to undertake and complete this work.

CHAPTER I
GENERAL INTRODUCTION

The Setting

The Bering Sea is a subarctic embayment of the North Pacific Ocean, separated from the Pacific by 1,200 miles of Aleutian Island arc and bounded by the land masses of Siberia to the west and Alaska to the east (Hood and Kelley, 1974). Nearly 44% of the Bering Sea consists of a wide and shallow continental shelf, which supports an organic production surpassed only by the upwelling areas of the eastern Pacific and eastern Atlantic Oceans (Hood and Kelley, 1974). A heavily exploited region in terms of fisheries, the Bering Sea ecosystem is currently the subject of intense scientific investigation seeking to understand those processes contributing to an "unusually efficient transfer of energy from primary producers to and between consumers" (Cooney, McRoy, Nishiyama, and Niebauer, 1979). This multi-disciplinary effort, represented by the PROBES (Processes and Resources of the Bering Sea Shelf) Program, has been examining physical oceanography, weather, nutrient distribution and regeneration, primary production, and upper trophic level dynamics in an attempt to formulate an ecosystem model of the southeastern Bering Sea. Other investigations conducted under the Outer Continental Shelf Environmental Assessment Program (OCSEAP) have provided quantitative data on the populations of important organisms in the various trophic levels of this ecosystem (Burns and Harbo, 1976; Lowry, Frost, and Burns, 1976; Fiscus, Braham, and Mercer, 1976; Pitcher and Calkins, in press). The shelf region of the ecosystem has been described as a "lake in the

sea," where unusual stability is influenced by extreme winter cooling and seasonal formation of sea ice (Goering, 1978). The seasonal ice cover of the Bering Sea shelf supports an undersurface algal mat "constituting a major standing stock of primary producers in the Bering Sea" (McRoy and Goering, 1974a) and provides an important substrate for pin-niped rest, reproduction, refuge, and food accessibility (Fay, 1974).

Sea ice covers the shelf entirely or in part from November through June, and influences productivity in all trophic levels (McRoy and Goering, 1974b). The late winter production of under-ice microalgae occurs earlier than the spring phytoplankton bloom of the ice-free water column, and may be of equal magnitude (McRoy, Goering, and Schiels, 1972; McRoy and Goering, 1974b). These overlapping pulses of primary production supply organic matter to the food chains leading to abundant invertebrate, finfish, and mammal populations which inhabit the region. From late March to July, large numbers of spotted seals (*Phoca largha*), among others, inhabit the ice front, exploiting the rich food supply, giving birth to young, mating, and molting (Burns, 1970; Fay, 1974; Shaughnessy and Fay, 1977). In June to August or September, harbor seals (*Phoca vitulina richardsi*) feed, bear young, mate, and renew their pelage at coastal habitats fringing the southern Bering Sea along the Aleutian Islands and northern Alaska Peninsula (Burns, 1970; Fay, 1974; Shaughnessy and Fay, 1977; Lowry, Frost, and Burns, 1979a; Pitcher and Calkins, in press). The timing and sequence, or phenology, of these events and their quantification are critical to a realistic evaluation of the trophodynamic scheme in this productive ecosystem.

Pinniped and Fishery Interactions in the Bering Sea

The trophodynamic interrelationships of pinniped populations and their food resources in the Bering Sea are not well understood. Although much data on food habits and related behavior of northern pinnipeds exists (Scheffer, 1950; Kenyon, 1956; Wilke and Kenyon, 1957; Scheffer, 1958; Spalding, 1964; Fiscus and Baines, 1966; Johnson, Fiscus, Ostenson, and Barbour, 1966; Lowry *et al.*, 1979a; Frost, Lowry, and Burns, 1979), few attempts have been made to define the niches occupied by these mammals in the complex trophic structure of the ecosystem. Interactions between seals and commercial fishery stocks have prompted detailed studies of the association between marine mammals and fisheries, such as the ecosystem model being developed by the National Marine Fisheries Service (McAlister, Sanger, and Perez, 1976; McAlister and Perez, 1977; Laevastu, 1978).

Pollock comprise one of the major foods of harbor, spotted, and ribbon (*Phoca fasciata*) seals in the Pribilof Islands area of the southeastern Bering Sea (Lowry *et al.*, 1979a) and are important also in the diet of fur seals (*Callorhinus ursinus*) and sea lions (*Eumetopias jubatus*) inhabiting this region (Scheffer, 1950; Lowry *et al.*, 1979a). Harbor and spotted seals also feed heavily on herring during summer months nearshore (Lowry *et al.*, 1979a).

Probably overfishing has caused the decline of the eastern Bering Sea pollock fishery from the peak catch of over 1.8×10^6 metric tons in 1972 to a total allowable catch of 9.5×10^5 metric tons in 1977 (National Marine Fisheries Service, 1977). Recently, it has been

estimated that the biomass of pollock and herring consumed by Bering Sea harbor and spotted seals exceeds the present catch of each fishery (Lowry *et al.*, 1979a). McAlister *et al.* (1976) estimated the finfish component of the total food consumption of harbor seals, spotted seals, ringed seals (*Phoca hispida*), ribbon seals, bearded seals (*Erignathus barbatus*), fur seals, and sea lions in the eastern Bering Sea to be 2×10^6 to 3×10^6 metric tons, a figure "approximately equal to, or slightly larger than," the present commercial fisheries combined.

Recent passage of the Marine Mammal Protection Act in 1972 and the Fishery Conservation and Management Act in 1976 has made clear the Federal Government's recognition of the need to conserve and manage marine resources. However, the two acts also have presented mutually conflicting policies which may inhibit effective systems management of marine mammal and fishery stocks in the southeastern Bering Sea (Lowry *et al.*, 1979a). Both acts have the management goal of maintaining optimum sustainable populations of species, yet management programs for marine mammals in Alaska have not been implemented and commercial fishing effort is expanding (Lowry *et al.*, 1979a). Before adequate management programs can be developed, knowledge of environmental carrying capacity for a species must be gained from study of trophic level relationships and population assessment. Intensive fisheries such as those for pollock and herring in the Bering Sea may precipitate a "re-adjustment of marine mammal populations" to levels significantly lower than current ones (Lowry *et al.*, 1979a).

Present assessment of pinniped food habits and estimates of nutritional requirements are based on studies of both wild and captive individuals. The natural food of pinnipeds has been determined primarily by examining stomach and intestinal contents, feces and vomitus, and observing animals feeding. Many researchers believe natural feeding to be regulated mostly by circumstance, the animals tending to exploit those species "that are most abundant, within their geographical range, and most easily captured and devoured" (Keyes, 1968). Frequency of feeding and daily nutritional requirements of wild pinnipeds have not been directly determined. Daily consumption rates ranging from 6 to 8% of total body weight have been estimated for wild seals, on the basis of calculations for captive animals (Scheffer, 1950; Sergeant, 1973; Geraci, 1975). McAlister *et al.* (1976) assumed a daily consumption rate of 7.5% of body weight in order to derive estimates of seasonal consumption from biomass for pinnipeds in the eastern Bering Sea. Over half of the institutions contacted by Hubbard (1968) fed 6 to 10% of the animal's body weight per day. Growing, pregnant, and lactating seals were given food portions greater than 10% of their body weight (Hubbard, 1968). Spalding (1964) reviewed estimates of food requirements for captive fur seals, sea lions, and harbor seals as reported in the literature, noting a range of 2 to 7% of body weight consumed daily, with an average daily food intake of 5%. An average value of 6% body weight per day was obtained when maximum weights of stomach contents of 2 to 11% from wild specimens were included in the data (Spalding, 1964). Miller (1978) suggested a value of 14% body weight as the daily food requirement of

pelagic subadult fur seals. The great disparity in estimates reflects the general uncertainty of food consumption rates in wild pinnipeds and may result in unrealistic conclusions depending on the estimate used (Lowry *et al.*, 1979a). Season, reproductive status, age, physical condition, activity, and sex have been correlated with food intake either inadequately or not at all. Values of food consumption by captive animals that are used as estimates for wild pinnipeds do not account for the caloric contents of different diets. The diet represented by consumption figures often has been overlooked: 7% may apply to a relatively low-fat diet such as pollock, while only 5% may be sufficient for caloric equivalence with a high-fat diet such as herring (Geraci, 1975). It seems clear that, in order to appraise the impact of a pinniped species on its prey organisms realistically, these factors must be considered in the context of an annual energy budget for the species.

The Framework of Pinniped Energetics

The study of mammalian bioenergetics has had early and wide application in programs devoted to increasing production efficiency of domestic livestock (Brody, 1945) and, more recently, has been directed at the evaluation of human impact on wild populations of mammals through determination of mutual energy sources and needs (Moen, 1973). At the organismal and populational levels, bioenergetics is governed by the same thermodynamic principles which dictate physical energy transfers and transformations. The individual or population is represented by a thermodynamic system which exchanges matter and energy (heat and work)

with its surroundings, is assumed to maintain equal rates of matter and energy influx and efflux (a steady state), and is irreversible in that internal work is continually converted to thermal energy and dissipated as heat (Wiegert, 1968). From examination of energy flow in an animal, an energy budget is derived which must be balanced and may be extrapolated to the natural population after population structure, stability, growth and productivity, and energy requirements have been considered. It is impossible to specify a continuous steady-state condition with individual living organisms, since growth and daily existence involve rapidly changing thermodynamic variables. However, one may describe these transitory states as the establishment of one steady state after another, integrating them over time (Gallucci, 1973), or simply recognize the error involved and qualify any conclusions derived from energy budget calculations (Wiegert, 1968).

The concept of energetic efficiency has had many interpretations in the literature, but in trophodynamic studies Kozlovsky's (1968) definition seems most appropriate. He relates ecological efficiency to the idea of transfer efficiency, or the ratio of energy available to trophic level $n + 1$ to the energy ingested or removed from trophic level $n - 1$ by trophic level n . Kozlovsky (1968) has noted a decrease in ecological efficiency above trophic level II (primary consumers), "so that values below 10% should not be considered anomalous." In energetic studies of a single animal population, the gross efficiency expressed as the ratio of yield (or production) to ingestion (Slobodkin, 1960) is a useful measure of ecological efficiency.

Measures of Energy Expenditure

In formulating the energy budget for an animal, whether as a means of identifying individual variation or as a basis for extrapolation to the larger population, the rate of energy metabolism "integrates more aspects of animal performance than any other physiological parameter" (Bartholomew, 1977). Measurements of whole animal metabolism used most frequently in energetics studies are indirect calorimetry and food consumption trials (Gessaman, 1973; Mautz and Fair, 1980).

Indirect calorimetry involves measurement of the oxygen consumed and carbon dioxide produced by an individual and calculation of its heat production through use of the respiratory quotient or RQ. The RQ, or ratio of carbon dioxide produced to oxygen consumed, indicates the type of substrate oxidized by the body (protein, carbohydrate, fat, or a combination of these) and the heat derived per volume of oxygen consumed (caloric equivalent of oxygen). The standard measurement in indirect calorimetry is basal metabolic rate or BMR (also referred to as standard metabolic rate, SMR), the heat production of an animal under rigorously defined criteria to allow comparison with other species (Hoch, 1971). These criteria specify that the animal be in good nutritive condition, in a state of muscular repose (but not asleep), postabsorptive (at least 12 hours fasted), and in a thermoneutral environment (Church and Pond, 1974; Maynard, Loosli, Hintz, and Warner, 1979). Four major components have been identified in metabolic studies with captive animals:

- (1) the specific dynamic action of food, or the energy cost of assimilation and digestion (SDA);
- (2) the energy cost of activity;

- (3) the energy cost of thermoregulation; and
- (4) the energy cost of production, which includes tissue growth, storage, and reproduction.

Levels of metabolism commonly reported in the literature are summations of BMR and these components, and are presented in Table 1.

The food consumption method measures productivity in addition to metabolism. It is based on the amount of food energy available to an animal or trophic level, influenced by a variety of factors related in the energy balance equation:

$$NE = GE - (FE + UE + SDA) = NE_p + NE_m \quad (1)$$

where NE equals net food energy, GE equals gross food energy, FE equals fecal energy, UE equals urinary energy, SDA equals specific dynamic action of food (not detectable by the food consumption method), and NE_p and NE_m are those components of the net food energy associated with production and maintenance, respectively. Net energy is estimated from the difference in caloric content of food consumed (gross energy) and material egested and excreted (feces and urine) by a caged animal over a period of several days (Gessaman, 1973). Food is provided *ad libitum* and the animal is free to move within its cage. When NE_p is negligible (weight is constant and other forms of production are not occurring), and space for movement and activity are equivalent in both food consumption and indirect caloric measurements,

$$NE = EM \approx ADMR \quad (2)$$

where EM equals the energy cost of free existence (Gessaman, 1973), and

TABLE 1. Levels of metabolism commonly reported in the literature.
(adapted from Gessaman, 1973 and Bartholomew, 1977).

I.	Fasting Metabolism: $FMR = BMR + \text{activity}$
II.	Resting Metabolism: $RMR = BMR + SDA + \text{thermoregulation}$
III.	Maintenance Metabolism: $MMR = BMR + SDA + \text{thermoregulation} + \text{activity}$
IV.	Average Daily Metabolism: $ADMR = BMR + SDA + \text{thermoregulation} + \text{activity} + \text{production}$

ADMR equals average daily metabolic rate expressed as calories with use of the appropriate caloric equivalent of oxygen.

The turnover rates of body water labeled with D_2O and $H_2^{18}O$ (doubly-labeled water, or $D_2^{18}O$) and radiotelemetered heart rate also have been used as indirect measures of free-living animal metabolism. The doubly-labeled water method has been validated for many species, but can be expensive and time-consuming (Mullen, 1973). It is based on the fact that the oxygen of expired carbon dioxide is in isotopic equilibrium with the oxygen of body water (Lifson, Gordon, Visscher, and Nier, 1949). The hydrogen in body water is lost mainly as water, while the oxygen is lost both as water and carbon dioxide. These two components of body water are labeled with stable isotopes of hydrogen (deuterium) and oxygen (oxygen-18) and injected into the animal's body. The difference between hydrogen isotope and oxygen isotope loss rates is a measure of carbon dioxide production and thus metabolic rate (LeFebvre, 1964; Nagy, 1975). Radiotelemetered heart rate, used for many years in studies of human energetics, has been of limited value in the estimation of energy expenditure from heart rate-metabolism regressions (Brockway and McEwan, 1969; Mautz and Fair, 1980). The heart rate-energy expenditure relationship varies among individuals within the same species and between days for the same individual (Morhardt and Morhardt, 1971). Various stimuli affect heart rate without causing concurrent changes in metabolism (Johnson and Gessaman, 1973). In some species, heart rate can be a reliable index of energy expenditure when separate regressions of oxygen consumption on heart rate specific for season are established for different activity levels over long time periods (Pauls, 1980).

Estimates of Free Existence Metabolism

A detailed survey of experiments estimating the energy expenditure of birds and mammals in their natural environments has been made by Gessaman (1973).

In small mammals, estimates of free-living metabolism have been derived from measurements of ADMR in several rodents (Pearson, 1947; Wiegert, 1961) and least weasels, *Mustela* (Golley, 1960), and measurements of RMR + activity in harvest mice, *Reithrodontomys* (Pearson, 1960) and three species of field mice, *Peromyscus* (McNab, 1963). The product of measured food consumption and assimilation efficiency also has been used as an approximation of free energy expenditure in tree squirrels, *Tamiasciurus* (Smith, 1968). Mullen (1970, 1971a, 1971b) measured the daily energy budgets of free-living pocket mice (*Perognathus*), canyon mice (*Peromyscus*) and kangaroo rats (*Dipodomys*) in Nevada by injecting live-trapped animals with D_2O and $H_2^{18}O$, obtaining blood samples, and releasing them to the study area for later recapture and blood sampling throughout the year. Newman (1971) computed annual and seasonal energy flow for a salt marsh shrew population (*Sorex*) in California from estimates of ADMR + RMR. Values of RMR + activity were used to calculate energy flow in 13 species of mammals inhabiting a desert community in Arizona (Chew and Chew, 1970). Odum, Connell, and Davenport (1962) measured existence metabolism with food consumption trials for a field mouse (*Peromyscus*) population and doubled their value to estimate free-living energy flow. Randolph (1972) estimated the seasonal energy requirements of a short-tailed shrew (*Blarina*) population by incorporating

studies of thermal balance, activity metabolism, food consumption, and assimilation efficiency in individual shrews in a model of the shrew predator-prey system. Energy flow in a *Peromyscus* population was modeled by Baar and Fleharty (1976) from estimates of RMR + activity in individual mice subjected to seasonal temperature variations in a nesting chamber, and daily and seasonal variation of temperature and photoperiod in an adjoining respirometer-activity chamber.

As Gessaman (1973) indicates in his review, few studies have been done on the energetics of large wild mammals, although much information exists on the energy metabolism and food consumption of domestic species. Many studies of wild species did not attempt to estimate the energy cost of free existence, but instead emphasized comparative metabolism or digestive efficiency in relation to maintenance and production (Gessaman, 1973). FMR and/or ME has been measured in roe deer (Weiner, 1977), red deer (Brockway and Maloiy, 1968), eland and wildebeest (Rogerson, 1968), and caribou (McEwan, 1970). Lamprey (1964) estimated the maintenance metabolism of average-weight individuals from 14 species of large African mammals as 3BMR from Hemmingsen's (1960) plot of BMR *versus* weight. Buechner and Golley (1967) estimated metabolism and food consumption for four age classes of Uganda kob from curves relating BMR to body weight (Kleiber, 1961) and food consumption to body weight (Albritton, 1954). A value of 3BMR was used to approximate the active metabolism of each age class. The 3BMR estimate is in accordance with Brody's (1945) observation that 24-hour energy expenditure in horses and man, including rest periods, ranged from 1.3BMR to 4BMR, with 3BMR

equivalent to moderate work. Based on the measured oxygen consumption of other wild ruminants, Moen (1973) estimated values of 1.23BMR to 1.98BMR as the range of energy expenditure of adult white-tailed deer in five different activity regimes. From the activity pattern data of Struhsaker (1967) and calculations of Stevens (1970), Moen (1973) was able to show a seasonal variation of daily energy expenditure in mature elk and that the energy cost of activity for bull elk during the breeding season is directly related to their reproductive status in the herd.

Ecological Efficiency in Pinnipeds

Much recent interest in large mammal energetics has been focused on the assessment of pinniped energy requirements in relation to natural food resources and possible competition with commercial fisheries (Chapman, 1973; Sergeant, 1973; Boulva, 1973; McAlister *et al.*, 1976; Lavigne, Barchard, Innes, and Øritsland, 1977; Parsons, 1977; Gallivan, 1977; Miller, 1978). Ecological efficiency in pinniped populations has most often been expressed as the gross efficiency of production to ingestion, or production/ingestion x 100 (Sergeant, 1973; Boulva, 1973; Lavigne *et al.*, 1977; Parsons, 1977). A list of comparative values of ecological efficiency for pinnipeds and other mammals from various trophic levels is presented in Table 2. Sergeant (1973) calculated the ecological efficiency of northwest Atlantic harp seals at 0.5% based on biomass estimates of annual pup production and annual food intake. A higher value of 3.9% for harp seals was calculated by Lavigne *et al.* (1977) from estimates of 2BMR for individual energy requirements,

TABLE 2. Values of ecological efficiency (production/ingestion x 100) for species from various trophic levels (adapted from Lavigne *et al.*, 1977).

Species	Ingestion	Production	Efficiency	References
<i>Sylvilagus audubonii</i> (Desert cottontail rabbit)	1.08 kcal/m ² ·yr	0.03 kcal/m ² ·yr	2.80	Chew and Chew, 1970
<i>Microtus pennsylvanicus</i> (Meadow vole)	25.0 kcal/m ² ·yr	0.52 kcal/m ² ·yr	2.10	Golley, 1960
<i>Odocoileus virginianus</i> (White-tailed deer)	52.6 kcal/m ² ·yr	0.64 kcal/m ² ·yr	1.20	Davis and Golley, 1963
<i>Loxodonta africanus</i> (African elephant)	71.6 kcal/m ² ·yr	0.34 kcal/m ² ·yr	0.47	Petrides, Golley, and Brisbin, 1968
<i>Bos taurus</i> (Domestic cow)	14.3 kcal/m ² ·yr	0.86 kcal/m ² ·yr	6.00	Petrides <i>et al.</i> , 1968
<i>Phoca vitulina concolor</i> (Atlantic harbor seal)	7.04 x 10 ⁵ kcal/yr	4.2 x 10 ⁴ kcal/yr	5.90	Boulva, 1973
<i>Phoca groenlandica</i> (Harp seal)	--	--	0.50	Sergeant, 1973
<i>Phoca hispida</i> (Ringed seal)	--	--	3.80	Parsons, 1977

information on population structure, caloric content of food and seal tissue, reproductive energy requirements, and mortality estimates from hunting and natural causes. They suggested that Sergeant's (1973) use of pup production as the sole factor of yield, and of biomass approximations rather than energy values, may have resulted in an under-estimate of ecological efficiency for the species. Recalculation of Sergeant's (1973) data using energy values increased the efficiency estimate to 1.76% (Parsons, 1977). Incorporating a stable age distribution and including natural mortality as yield, Boulva (1973) estimated an ecological efficiency of 5.9% for eastern Canadian harbor seals, a value considered too high by others because of over-estimated food caloric content (Lavigne *et al.*, 1977). Lavigne *et al.* repeated Boulva's calculations using their values of food caloric content and obtained an estimate of 3.5%. Parsons (1977) used measurements of basal metabolic rate, digestibility and caloric content of important prey items, and estimates of energy losses from digestion and ingested and excreted materials to estimate maximum energy requirements of captive ringed seals. Applying this information in an analysis similar to Boulva's (1973), he computed an ecological efficiency of 3.8% for free-living Canadian Arctic ringed seals. These values of ecological efficiency compare favorably with estimates of 2 to 5% for mammals suggested by Steele (1974) and 2 to 3% for homeotherms (Turner, 1970). In a similar study on captive northern fur seals, Miller (1978) found an elevation of metabolism in water colder than 18°C and a consequent food intake requirement of 14% body weight per day for pelagic seals at an average water temperature of 5°C. He

concluded that present calculations of fur seal food consumption in the Bering Sea and North Pacific may have been under-estimated by a factor of 2.

Estimating the Energy Cost of Living for Bering Sea Harbor and Spotted Seals

The Species

Pacific harbor seals (*Phoca vitulina richardsi*) and spotted or larga seals (*Phoca largha*) of the Bering Sea comprise two large populations whose annual food consumption has been estimated at 9.7×10^5 metric tons over the eastern Bering Sea shelf (harbor and spotted seals combined) and 3.26×10^5 metric tons (harbor seals only) in the Aleutian area (McAlister *et al.*, 1976). McAlister *et al.* (1976) estimate the total Alaskan populations of harbor and spotted seals at 2.7×10^5 and 2.5×10^5 individuals, respectively. They estimate that approximately 6.5×10^4 harbor seals occupy the eastern Bering Sea shelf in summer, and an equal number in winter. Harbor seals are believed to number 8.5×10^4 in both seasons in the Aleutians. McAlister *et al.* (1976) estimate spotted seals to number 1.25×10^5 in summer and 2.5×10^5 in winter in the eastern Bering Sea shelf. Everitt and Braham (1978) have estimated a minimum abundance of 2.8 to 3.0×10^4 harbor seals from aerial censuses during the pupping season along the northern Alaska Peninsula and eastern Aleutian Islands from 1975 to 1977.

The harbor seal inhabits the North Pacific coast, with numerous local breeding populations from northwestern Baja California to the Gulf of Alaska, westward along the Aleutian and Commander Islands, and

southward along eastern Kamchatka to eastern Hokkaido, as shown by Figure 1 (Scheffer and Slipp, 1944; Fisher, 1952; Bishop, 1967; Marakov, 1967; Belkin, Kosygin, and Panin, 1969; Bigg, 1969; Brownell, DeLong, and Schreiber, 1974; Naito and Nishiwaki, 1973, 1975). These seals occupy nearly all inshore marine habitats along the coastal Gulf of Alaska, Alaska Peninsula, and northern Bristol Bay, and may occupy certain rivers and lakes on a seasonal basis (Lowry *et al.*, 1979a; Pitcher and Calkins, in press). During ice-free months, they may range as far north as Hooper Bay and the Yukon River Delta (Lowry *et al.*, 1979a). Harbor seal pups are born with a dark, adult-type coat, the white lanugo having been shed *in utero* before birth (Burns and Fay, 1973; Fay, 1974). Mating occurs soon after a lactation period lasting 3 to 6 weeks (Bishop, 1967; Bigg, 1969; Knutson, 1974; Johnson, 1976) and a short weaning period (Johnson, 1976). Mating is followed by molting, which has been observed to last about 5 weeks in captive individuals (Scheffer and Slipp, 1944).

The first life history study of harbor seals in the Gulf of Alaska was conducted by Bishop (1967) who collected preliminary data on population structure, productivity, and behavior at Tugidak Island and along the Kenai coast. Imler and Sarber (1947) collected data on food habits and population densities of harbor seals on the Copper River Delta in summer. Mathisen and Lopp (1963) noted harbor seal concentrations in the course of censusing Steller sea lions in Alaska from 1956 to 1958. The Alaska Department of Fish and Game (ADF&G) tagged over 4,000 harbor seal pups during commercial harvests from 1965 to 1972 to provide

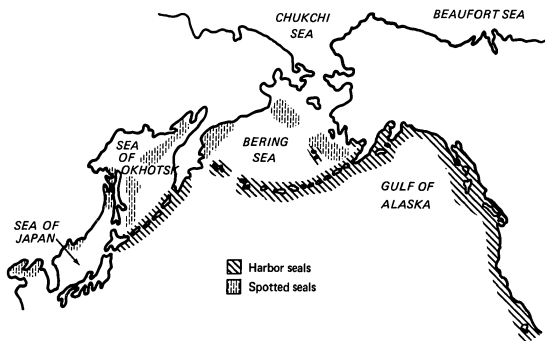


FIGURE 1. Distribution of breeding populations of harbor seals and spotted seals in the North Pacific (after Shaughnessy and Fay, 1977).

information on dispersal and known-age specimens for evaluation of age-determination techniques (Pitcher and Calkins, in press). The Alaska Department of Fish and Game also conducted surveys of seasonal distribution in Prince William Sound in 1973 and 1974 (Pitcher and Vania, 1973; Pitcher, 1977). Additional studies by Pitcher and co-workers provided data on population productivity, growth, physical condition, and food habits in Prince William Sound (Pitcher, 1977) and in the Gulf of Alaska from Yakutat Bay to Sanak Island (Pitcher and Calkins, in press). Food habits of both larga and harbor seals were studied by ADF&G in the southeastern Bering Sea (Lowry *et al.*, 1979a).

Other studies of the Pacific harbor seal include those of Fisher (1952) on life history and economics of seals in the Skeena River, British Columbia, and a food habits survey by Spalding (1964) also in British Columbia. Scheffer and Slipp (1944) made a detailed investigation of behavior, reproduction, food habits, and economics of harbor seals in Willapa Bay, Washington, and Newby (1973) also noted reproductive habits of harbor seals in Washington state.

Once considered a subspecies of *Phoca vitulina*, the spotted or larga seal (*Phoca largha*) is distinguished morphologically, ecologically, and physiologically (with regard to reproduction) from the harbor seal by differential cranial characteristics, its association during the breeding season with the pack ice of the Bering, Okhotsk, Japan, and Yellow Seas and its earlier (about two months) production of young and mating (Mohr, 1965; Chapskii, 1967, 1969; Shaughnessy and Fay, 1977). During winter and spring in the Bering Sea, spotted seals inhabit the

southern fringe and front of the pack ice from northern Bristol Bay to the Koryak and Kamchatka coasts (Fay, 1974; Shaughnessy and Fay, 1977). The spotted seal's association with the ice front may be as much a consequence of feeding behavior as of inability to penetrate heavy ice (Fay, 1974). In the Bering Sea, pups are born in late March and April on the ice with a white, woolly lanugo (Burns, 1970; Burns and Fay, 1973; Burns, Ray, Fay, and Shaughnessy, 1972; Fay, 1974; Shaughnessy and Fay, 1977). The seals form widely-spaced "family groups," consisting of an adult male, a female, and a pup, and are assumed to be territorial (Burns *et al.*, 1972; Fay, 1974). The seals disperse inshore in the summer months; some of them migrate to the Chukchi Sea as far as the northern coast of Alaska, and return to the Bering ice front in autumn (Fay, 1974). The birth of pups in the Okhotsk and Japan Seas varies latitudinally with the extent and stability of the pack ice (Shaughnessy and Fay, 1977).

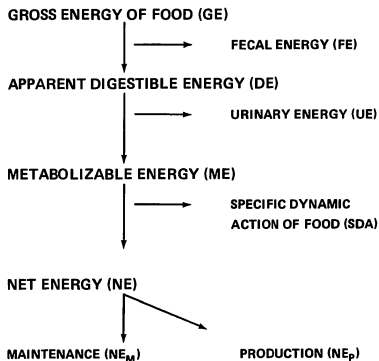
As with the harbor seal, the biology and ecology of the spotted seal has been little studied until recently. The postnatal growth and reproductive development of *P. largha* were investigated by Tikhomirov (1971). Prenatal and postnatal growth of spotted seals in the waters surrounding Hokkaido were examined from 1968 to 1971 by Naito and Nishiwaki (1972). Burns (1970) discussed the ecology, behavior, and morphology of spotted seals in relation to the distribution of other ice-inhabiting pinnipeds of the Bering and Chukchi Seas. The adoption of a strange pup by a female *largha* was reported by Burns *et al.* (1972) who suggested that the spatial isolation of parturient females precluded

the necessity for mother-pup recognition. Shaughnessy (1975) was not able to detect differences in blood proteins of spotted and harbor seals by gel electrophoresis. Shaughnessy and Fay (1977) reviewed the nomenclatural history and taxonomy of North Pacific harbor seals in depth and recommended that the spotted seal be given specific rank. The feeding habits of spotted seals in the Okhotsk Sea have been reported by Wilke (1954) and Fedoseev and Bukhtiyarov (1975), and in the southeastern Bering Sea by Lowry *et al.* (1979a). Population structure, mortality, and distribution was assessed by Popov (1976) in a status report on ice-inhabiting seals of the USSR and adjacent waters. Beier and Wartzok (1979) made a detailed analysis of the mating behavior of captive *Phoca largha*, the first of its kind on any seal.

The Problem

A simplified budget of energy utilization in an individual non-ruminant mammal is illustrated by Figure 2 (Harris, 1966; Moen, 1973; Kleiber, 1975). The goal of this study was quantification of the various components of this basic plan for individual captive Bering Sea harbor and spotted seals, with ultimate extrapolation to the wild population of each species.

GROSS ENERGY BUDGET



1. **BASAL METABOLISM (BMR)**
2. **THERMOREGULATION**
3. **ACTIVITY**
 - A) **SLEEPING**
 - B) **SWIMMING**
 - C) **DIVING**
 - D) **MAXIMUM WORK ($\dot{V}_{O_2 \text{ MAX}}$)**

1. **ENERGY STORAGE (FAT)**
2. **GROWTH (LBM)**
3. **MOLT**
4. **REPRODUCTION**

FIGURE 2. A simplified budget of energy utilization in an individual non-ruminant mammal (adapted from Harris, 1966; Itoen, 1973; Kleiber, 1975).

CHAPTER II

ENERGY ASSIMILATION: PROXIMATE COMPOSITION, GROSS ENERGY, AND CONSUMPTION OF FOOD



Introduction

The type, amount, nutrient composition, and gross energy content of food are basic to the formation of a mammalian energy budget. Data on daily food intake and nutritional requirements are often obtained from studies of captive animals, while information on food preferences and seasonal feeding habits is derived from observation and gut content analyses of wild mammals. The nutrient composition of a food refers to the proportion of protein, carbohydrate, and fat it contains, which are estimated from chemical analyses specific for each constituent (Horwitz, 1970) and included in the description "proximate composition of analysis" (Geraci, 1975). Gross food energy (GE), or the energy content in kilocalories per gram, is indirectly estimated from the caloric equivalents of protein, carbohydrate, and fat comprising the food, or directly determined by combustion of the food in a bomb calorimeter (Paine, 1971).

Finfish comprise the main dietary component in most pinniped species that have been examined (McAlister *et al.*, 1976). Fishes contain 66 to 84% moisture, or preformed water, and have relatively high proportions of protein and fat with negligible amounts of carbohydrate (Jacquot, 1961; Geraci, 1975). In many species of fishes, there is a strong negative correlation between fat and water content (Jacquot and Creach, 1950; Jacquot, 1961). Three general categories of fishes have been recognized on the basis of lipid content: fatty (e.g., herring, mackerel, salmon, shad), semi-fatty (e.g., bass, halibut, mullet, shark), and lean (e.g., cod, haddock, pollock, smelt). The proximate composition of typical fatty, semi-fatty, and lean fishes are given in Table 3, adapted

TABLE 3. Average composition of typical fatty, semi-fatty, and lean fishes (after Jacquot, 1961).

Category	% Moisture	% Protein	% Fat	% Ash
Fatty Fish*	68.6	20.0	10.0	1.4
Semi-fatty Fish**	77.2	19.0	2.5	1.3
Lean Fish***	81.8	16.4	0.5	1.3

* e.g., herring, mackerel, salmon, shad.

** e.g., bass, halibut, mullet, shark.

*** e.g., cod, haddock, pollock, smelt.

from the work of Jacquot (1961). The range of fat content within species and between individuals may be considerable because of the effects of age, sex, location, and season (as related to sexual development and feeding). In species which feed on plankton, the lipid content of the fish closely follows that of its prey, which may reach levels as high as 10% during certain seasons (Venkataraman and Chari, 1953). Stoddard (1968) reported a variation in fat content of Atlantic herring (*Clupea harengus harengus*) of 2 to 4% in spring to over 15% in early winter. Variation of fat content in capelin (*Mallotus villosus*) from 1% in spring to nearly 23% in fall is attributed to fat loss while fasting during spawning migrations in late spring, with fat replenishment during vigorous feeding after spawning (MacCallum, Adams, Ackman, Ke, Dyer, Fraser, and Punjamapirom, 1969; Jangaard, 1974). Because fat combustion provides more calories than that of protein or carbohydrate, fatty fishes will have higher caloric contents than equal amounts of semi-fatty or lean fishes.

The feeding habits of wild pinnipeds have been reviewed by several investigators and include observations of feeding and intestinal content analyses in harbor seals (Scheffer and Sperry, 1931; Barabash-Nikiforov, 1936; Imler and Sarber, 1947; Fisher, 1952; Wilke, 1957; Spalding, 1964; Kenyon, 1965; Morejohn, 1977; Pitcher, 1977; Pitcher and Calkins, in press; Cabbage, Calambokidis, and Carter, 1979), spotted seals (Inukai, 1942; Wilke, 1954; Gol'tsev, 1971; Fedoseev and Bukhtiyarov, 1972; Nikolaev and Skalkin, 1975; Lowry *et al.*, 1979a), ringed seals (Dunbar, 1941; McLaren, 1958; Johnson *et al.*, 1966; Fedoseev, 1965; Frost *et al.*,

1979), harp seals (Fisher and Mackenzie, 1955; Myers, 1959; Sergeant, 1973), ribbon seals (Arsen'ev, 1941), Weddell seals (Bertram, 1940; Ray, 1966), bearded seals (Lowry, Frost, and Burns, 1979b), northern fur seals (Clemens and Wilby, 1933; Wilke and Kenyon, 1952, 1957; Scheffer, 1950; Kenyon, 1956; Spalding, 1964; Panina, 1971), Steller sea lions (Wilke and Kenyon, 1952; Nesterov, 1964; Panina, 1966; Fiscus and Baines, 1966), and California sea lions (Scheffer and Neff, 1948; Fiscus and Baines, 1966; Bowlby, 1979). Seasonal variations in food preference and stomach volume have been noted which correlate with availability of prey and reproductive condition of the species. Reduced feeding has been observed during lactation, breeding, and molting in some pinnipeds (McLaren, 1958; Hart and Fisher, 1964; Spalding, 1964; Johnson *et al.*, 1966; Mansfield, 1967; Hubbard, 1968; Gol'tsev, 1971; Sergeant, 1973) and this corresponds to seasonal changes in body fatness and condition (Imler and Sarber, 1947; McLaren, 1958; Johnson *et al.*, 1966; Bishop, 1967; Lønø, 1970; Sergeant, 1973; Pitcher, 1977; Pitcher and Calkins, in press). Important prey of harbor and spotted seals are given in Table 4.

Food consumption rates for captive pinnipeds have been summarized by Keyes (1968) who contacted 34 zoos and aquaria maintaining marine mammals. He found that more than half of these institutions fed 6 to 10% of the animal's body weight per day, with larger species (elephant seals, Steller sea lions) and individuals receiving 1.6 to 3.0% of body weight per day. Young harp seals and hooded seals (*Cystophora cristata*) maintained at Oslo were initially fed at 3% of body weight per day at 2 months of age, then increased to 5% when 5.5 months old (Blix, Iversen,

TABLE 4. Important prey of harbor and spotted seals listed in order of decreasing occurrence. N = total number of seals examined; (n) = number of seals with food present in gut.

Species	Location & Date	N (n)	Prey	Source
<i>Phoca vitulina richardsi</i>	Washington: Puget Sound (Dec. 1927-Aug. 1930)	100 (81)	Flounder Herring Hake Sculpins Crab Shrimp Squid Pollock	Scheffer and Sperry, 1931
	USSR: Komandorski Is. (Winter-Spring)	--	Octopus Crab Sipunculids	Barabash- Nikiforov, 1936
	(Summer-Fall)	--	Sculpins Greenling	
	Alaska: Copper River (May-June, 1945)	(67)	Eulachon	Imler and Sarber, 1947
	Southeastern (1945-46)	(99)	Pollock Cod Herring Flounder Salmon Sculpins	
	British Columbia: Fraser River, Queen Charlotte Is. and Skeena River	50 (20)	Salmon Herring Rockfish Unident. fish Octopus Shrimp Crab	Fisher, 1952
	Alaska: Amchitka Is.	7	Greenling Octopus Crab Pollock Cod	Wilke, 1957

TABLE 4. Continued.

Species	Location & Date	N (n)	Prey	Source
<i>Phoca vitulina richardsi</i>	British Columbia	126 (69)	Salmon Squid Octopus Herring Flatfish Rockfish	Spalding, 1964
	Alaska: Amchitka Is. (Mar.)	(11)	Atka mackerel Octopus	Kenyon, 1965
	California: Monterey Bay	--	Top smelt White croaker Spotted cusk eel English sole Tongue sole	Morejohn, 1977
	Alaska: Prince William Sound (all seasons 1975- 76)	151	Pollock Herring Squid Octopus Pacific cod Capelin Tomcod Salmon Saffron cod	Pitcher, 1977
	Copper River (June 1975)	45	Eulachon	
	Alaska: Unalaska Is. (Apr. 1972)	(3)	Pollock Pacific cod	Lowry, Frost, and Burns, 1979a
	Adak Is. (July- Aug. 1973)	(6)	Pandalid shrimp Mysids Pacific cod Sculpins Crangonid shrimp	

TABLE 4. Continued.

Species	Location & Date	N (n)	Prey	Source
<i>Phoca vitulina richardsi</i>	Atka Is. (Aug. 1973)	(2)	Octopus	Lowry <i>et al.</i> , 1979a
	SW Bristol Bay (Mar. 1976)	(1)	Capelin	
	Alaska: Prince William Sound	122 (83)	Pollock Herring Squid Tomcod Capelin	Pitcher and Calkins, in press
	Kenai coast (Resurrection Bay - Pt. Adam)	52 (30)	Pollock Herring Sandfish Capelin Tomcod	
	Lower Cook Inlet (Kachemak and Kamishak Bays)	23 (17)	Octopus Eulachon Shrimp Capelin	
	Alaska Peninsula (Puale Bay, Shumagin, Is., Sanak Is.)	9 (6)	Octopus Pollock Sandfish Cod Sculpins	
	Kodiak Is. (Barren Is. - Chirikof Is.)	192 (102)	Octopus Capelin Pollock Flatfishes Cod Sandlance Herring	
	Gulf of Alaska 0-12 month old seals	(13)	Capelin Pollock Shrimp Sandlance Tomcod	

TABLE 4. Continued.

Species	Location & Date	N (n)	Prey	Source
<i>Phoca vitulina richardsi</i>	Washington; Hood Canal	--	Pacific hake Plainfin midshipman	Cabbage, Calambokidis, and Carter, 1979
	N. Puget Sound	--	Blackbelly eelpout Pacific herring	
	S. Puget Sound	--	Staghorn sculpin Pacific hake	
	USSR: Commander Is. (Aug. 1974)	51 (16)	Octopus Unident. fish Squid	Burns and Gol'tsev, in prep.
	Alaska: W. Aleutian Is. (July-Aug.) weanling seals	43 (17)	Mysids Pandalid shrimp Octopus Crangonid shrimp Sculpins Pacific cod	
	E. Aleutian Is. (April)	(3)	Pollock Pacific cod	
	Pribilof Is. (April)	(8)	Pollock Cod	
<i>Phoca largha</i>	Japan: Hokkaido (May)	--	Herring	Inukai, 1942
	Okhotsk Sea (April 1949)	21 (19)	Pollock Herring Octopus Squid	Wilke, 1954

TABLE 4. Continued.

Species	Location & Date	N (n)	Prey	Source	
<i>Phoca largha</i>	NW Bering Sea (April-June, 1966-68) seals, 1st yr.:	319	Amphipods	Gol'tsev, 1971	
			Algae		
			Shrimp		
		seals, 1-4 yrs.:		Sandlance	
				Flatfish	
				Saffron cod	
				Arctic cod	
	seals, 5+ yrs.:		Sandlance		
			Saffron cod		
			Pandalid		
			shrimp		
			Octopus		
			Crab		
			Flounder		
			Sculpins		
	Northern and Eastern Okhotsk Sea (Spring)	23	Pollock	Fedoseev and Bukhtiyarov, 1972	
			Saffron cod		
			Sandlance		
			Euphausiids		
			Decapod		
			crustaceans		
	USSR: Terpenie Bay	7 (3)	Unident. fish	Nikolaev and Skalkin, 1975	
			Shrimp		
			Crab		
			Octopus		
	Alaska: Mekoryuk (May 1975)	(8)	Greenling	Lowry <i>et al.</i> , 1979a	
			Crangonid		
			shrimp		
			Herring		
			Sculpins		
	NW Pribilof Is. (Mar. 1977)	(1)	Octopus		
			Eelpout		
			Pollock		
	W. St. Matthew Is. (May 1977)	(1)	Capelin		

TABLE 4. Continued.

Species	Location & Date	N (n)	Prey	Source
<i>Phoca largha</i>	W. Bristol Bay (April 1977)	(7)	Capelin Pollock	Lowry <i>et al.</i> , 1979a
	W. Nunivak Is. (May 1977)	(2)	Capelin Herring	
	SW Bristol Bay (Mar. 1976)	(4)	Capelin	
	USSR: Karaginski Bay	68	Sandlance Herring Octopus Shrimp	Bukhtiyarov, Frost, and Lowry, in prep.
	Gulf of Anadyr	42	Arctic cod Pollock Sandlance Octopus Crab Shrimp	
	Combined areas seals, 1st yr.:	27	Algae Sandlance Shrimp	
	seals, 1-4 yrs.:	21	Sandlance Unident. fish Shrimp Octopus Arctic cod Flatfish Algae Mollusks Crab	
	seals, 5+ yrs.:	35	Octopus Unident. fish Sandlance Shrimp Herring Arctic cod Crab Greenling Sculpins	

TABLE 4. Continued.

Species	Location & Date	N (n)	Prey	Source
<i>Phoca largha</i>	seals, 5+ yrs.:		Pollock Saffron cod Mollusks	Bukhtiyarov <i>et al.</i> , in prep.
	Southcentral Bering Sea	5	Pollock Eelpout Prickleback Sculpins	
	Southeastern Bering Sea	14	Capelin Pollock Sculpins Herring Flatfish Saffron cod Arctic cod	
	Northern Bering Sea	12	Arctic cod Saffron cod Capelin Sculpins Herring Sandlance Flatfish Pollock Eelpout	

and Päsche, 1973). Spotted seals maintained at Johns Hopkins University, Baltimore, were fed an average of 13% of body weight per day as yearlings, with food intake decreasing steadily with age to 3% at 9 years (Ashwell-Erickson, Elsner, and Wartzok, 1979). Data on food intake requirements during breeding and molting in captive pinnipeds are lacking, as is information on the effects of activity levels and plane of nutrition.

In this study, the gross energy content and nutrient composition of pollock and herring, two finfish important in the diets of Bering Sea harbor and spotted seals, were compared. Long-term observations of food consumption and body weight of captive harbor and spotted seals fed these fishes were related to the compositional data to estimate the gross energy requirements of wild harbor and spotted seals.

Methods and Materials

Proximate Composition and Gross Energy of Food

From November 1975 to January 1978, fresh frozen herring in eight lots of 1000 kg each were supplied by New England Fish Company of Kodiak, Alaska. Additional fresh frozen herring was provided by Seward Fisheries of Seward, Alaska in three lots of 1000 kg each from February to October 1978. These fishes were fed to the seals throughout their captivity. Approximately 200 kg of fresh frozen pollock were supplied by New England Fish Company in November 1978. These fishes were used in studies of digestibility and nitrogen balance in the seals. Fishes were stored at -20°C ; when needed, 2-day feeding allotments were air-thawed at $+4^{\circ}\text{C}$

in plastic bags. The weight range of individual pollock was approximately 150 to 250 g, and that of herring was 50 to 150 g. Random samples of whole fishes from three lots of herring (Lot A from June 1977, Lot B from November 1977, and Lot C from February 1978) and one lot of pollock (November 1978) were kept frozen in airtight plastic containers at -50°C for later analysis.

Five samples of whole fish from each lot were analyzed for moisture, protein, fat, and energy content. Percent moisture was calculated as the difference between the wet and dry weights of each fish, freeze-dried according to the method of Horwitz (1970). Individual freeze-dried fishes were homogenized by means of a mortar and pestle and stored in aluminum pans in vacuum desiccators with CaSO_4 (Hammond Drierite) at room temperature until analyzed. The protein composition of pollock and herring was determined by analysis of nitrogen content in five 15-mg samples of each freeze-dried, homogenized fish by the Dumas method (Horwitz, 1970) with an automated nitrogen analyzer of $\pm 0.2\%$ accuracy (Coleman Model 29B, Coleman Instruments Division, Perkin-Elmer Corporation). The nitrogen content of each sample was expressed as percent by weight, based on the original wet weight of the fish, and values were multiplied by a factor of 6.25 to yield corresponding percent protein.

Total lipid was extracted from five samples of each freeze-dried, homogenized fish using a modified, quantitative chloroform-methanol-water extraction technique (Bligh and Dyer, 1959). To 1 g of sample in a 50-ml centrifuge tube with a Teflon-lined screw cap (Kimble Glass) was added 4 ml distilled water, 10 ml methanol, and 5 ml

chloroform. This mixture was shaken by hand for one minute, followed by the addition of 5 ml chloroform and 9 ml distilled water, and inverted (not shaken) 12 times. All tubes were then centrifuged for 15 minutes at $>1500g$. After centrifugation, a biphasic system was observed in each tube, consisting of a lower chloroform layer containing the lipid, and a methanol-water layer of non-lipid material at the top. The methanol-water layer was removed by aspiration as much as possible, and a 5-ml aliquot pipetted from the remaining chloroform layer into a tared 25-ml Erhlemeyer flask. The aliquot was evaporated to dryness in a 50°C waterbath, facilitated by a stream of nitrogen. The residue was dried over P_2O_5 in a vacuum dessicator and the dry weight determined. Five milliliters of chloroform were added to the residue to detect the presence of non-lipid material (insoluble). If non-lipids were present, the chloroform was carefully decanted and the flask rinsed three times with chloroform. The dry weight of the residue was determined and subtracted from the initial weight. The sample lipid content was calculated according to the equation:

$$\begin{aligned} \text{Total lipid} &= \frac{\text{weight of lipid in aliquot} \times \text{volume of chloroform layer}}{\text{volume of aliquot}} \\ &= \frac{\text{weight of lipid in aliquot} \times 10}{5} \end{aligned} \quad (3)$$

and expressed as percent lipid based on the original wet weight of the fish.

The gross energy content in cal/g of each food item was determined by combustion of five 1-g samples of each freeze-dried, homogenized fish in a bomb calorimeter (Parr Series 1200 Adiabatic Calorimeter),

according to standardized techniques (Schneider and Flatt, 1975). Percent ash was computed as the difference between the weight of sample before and after combustion, in relation to the total fish wet weight. Mean values were computed for the nutrient composition and energy content of each food, and were considered to be significantly different from each other if $P < 0.05$ according to Student's "t" distribution.

Food Consumption and Body Weight of Captive Seals

The food intake and body weight of 11 Pacific harbor seals (*Phoca vitulina richardsi*) and three spotted seals (*Phoca largha*) were monitored continuously. Two harbor seals, captured as yearlings at Cold Bay, Alaska Peninsula, in 1975, comprised juvenile (3-year-old) and subadult (4-year-old) age groups. Nine harbor seals captured as weanlings in 1977 from a breeding colony on Ugak Island, near Kodiak in the Gulf of Alaska, formed the pup (0.2 to 0.7-year-old) age group. One of three weanling spotted seals, obtained during the cruise of the Russian sealing vessel *Zagoriansy* in the central Bering Sea in 1976, comprised the yearling (1-year-old) age group; the other two seals were included in the pup age group. There were male and female representatives in all except the yearling class. These 14 animals were raised in outdoor enclosures at the Institute of Arctic Biology Animal Facility in Fairbanks in 2.5 x 1.5 x 1.0 m pools with continuous fresh water inflow. During warm months water was circulated through a cooling system, entering the pools at a constant rate of 3 l/min and temperature of 12°C. To avoid freeze-up of plumbing and ice accumulation in the pools during cold months, the

cooling system was disconnected and water was allowed to flow at a rate of 6 l/min and temperature of 18°C.

The seals were fed herring (*Clupea harengus pallasii*) *ad libitum* daily, supplemented with vitamins and minerals (Geraci, 1972a, 1972b). Newly-captured seals were trained to eat whole dead fish by a force-feeding technique. As described by Johnson (1969), "the animal was straddled across its back and one hand held open the lower jaw while the other hand guided the fish carefully down the throat." The number of fish fed was increased gradually until the seal accepted fish on its own, usually after 2 weeks of force-feeding. The seals were weighed bi-weekly.

One male and one female spotted seal, captured as weanlings in the central Bering Sea in 1969 and reared at the School of Hygiene and Public Health Animal Facility, The Johns Hopkins University, Baltimore, comprised the 9-year-old (adult) class. These seals were housed indoors in a 3.5 x 3.5 x 1.5 m pool provided with continuously-filtered fresh water. Water temperature varied from 4 to 18°C, according to seasonal fluctuations. Light conditions were adjusted seasonally to simulate Bering Sea photoperiod. They were fed gutted Atlantic mackerel (*Scomber scombrus*) 6 days per week with vitamin and mineral supplements. Feeding was *ad libitum* until late 1976, when they were maintained on a constant-weight basis for another experiment. These animals also were weighed bi-weekly.

Results and Discussion

The proximate composition and gross energy of pollock and herring are presented in Table 5. Pollock had the highest percent moisture of the fishes analyzed, indicative of the inverse relationship between the degree of hydration and lipid content noted in many species of fishes (Jacquot and Creac'h, 1950; Brandes, 1954; Jacquot, 1961). Water, protein, and lipid contents of the three lots of herring examined were significantly different from each other ($P < 0.01$), possibly the result of interplay between seasonal, environmental, and physiological factors affecting the nutritional state of the catch. Food availability, weather, stage of sexual maturity, the spawning migration, and energy content of food are some of the factors contributing to observed variations in fat deposition in many fishes (Stoddard, 1968; MacCallum *et al.*, 1969; Jangaard, 1974). Energy content of the samples varied directly with fat content, ranging from 2418 cal/g wet weight in 18% fat herring to 1088 cal/g wet weight in 0.8% fat pollock. Fish fillets generally have less energy than whole fishes because subcutaneous fat has been removed.

Herring consumption, expressed as percent body weight, over 0.8, 1.5, and 2.5-year periods for a pup harbor seal, a yearling spotted seal, and a subadult harbor seal, respectively, are presented in Figure 3. Total body weights of these three animals are plotted against time in Figure 4. Food consumption by one yearling and two subadult seals was highest in winter and lowest in summer, with increasing body weight maintained throughout the year. On an *ad libitum* diet, the seals appeared to regulate their intake of herring to maintain their caloric requirements

TABLE 5. Proximate composition and energy content of whole pollock and herring fed to captive harbor and spotted seals.

Sample	Date Fed	% H ₂ O	% Protein	% Fat	% Ash	Energy Content	
						(cal/g dry)	(cal/g wet)
Pollock	Sept. 78	78.8±1.3	19.2±1.4	0.8±0.2	1.6±0.2	5135± 36	1088±59
Pacific Herring	Jun-Nov. 77 (Lot A)	71.7±0.2	20.0±1.1	5.1±0	2.3±0.5	5498±188	1564±34
	Nov. 77- Feb. 78 (Lot B)	66.8±0.5	18.5±0.8	12.2±1.1	2.4±0.1	6192± 57	2143±75
	Sept. 78 (Lot C)	64.0±0.5	16.3±0.2	18.0±0.5	2.0±0.2	6716± 42	2418±19

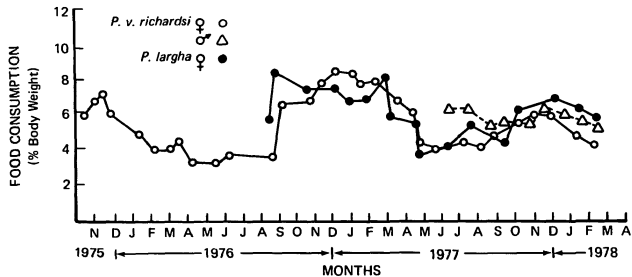


FIGURE 3. Variation in food consumption with time for one pup (Δ) harbor seal, one yearling (\bullet) spotted seal, and one subadult (\circ) harbor seal.

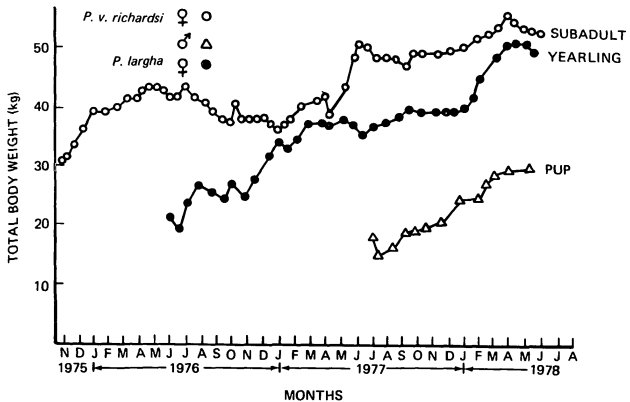


FIGURE 4. Variation of total body weight with time for one pup harbor seal, one yearling spotted seal, and one subadult harbor seal.

when the lots of fishes differed in energy content. For example, the total body weight of these seals increased as the caloric value of herring fed to them changed from a mean of 1564 (June to November 1977) to a mean of 2418 cal/g wet weight (November 1977-February 1978). As reported by Johnson (1969), the newly-captured pups initially lost weight while learning to eat dead fishes, but gained weight steadily once accustomed to eating them.

Mean annual food consumption of one male and one female spotted seal from ages 1 to 9 years, maintained on a diet of mackerel, is shown in Figure 5. Lacking information on the proximate composition of the mackerel fed, a value of 12% was assumed to be the average annual lipid content of the diet, based on the reported range in seasonal fatness of mackerel (Jacquot, 1961; Geraci, 1975). Food intake declined from a mean value of $13.0 \pm 2.5\%$ body weight consumed during the first year to a mean of $3.1 \pm 0.3\%$ at 9 years. These data were best described by linear regression of log transformed y variables, the equation of which was $y = 12.2(x + 1)^{-0.77}$ ($r = -0.95$). The declining food intake from 1 to 4 years corresponds with the steady decrease in rate of growth (body weight) during that period (Figure 6).

Summary

The caloric value of pollock and herring, two important finfish in terms of volume in the diets of Bering Sea harbor and spotted seals, varied directly with fat content and indirectly with moisture content. Herring samples from three separate lots ranged in gross energy content

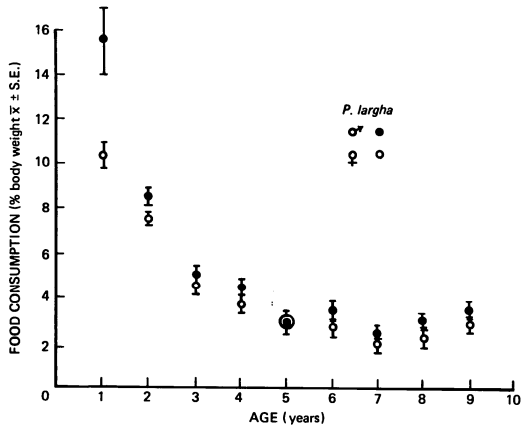


FIGURE 5. Mean annual food consumption of two spotted seals from ages 1-9 years.

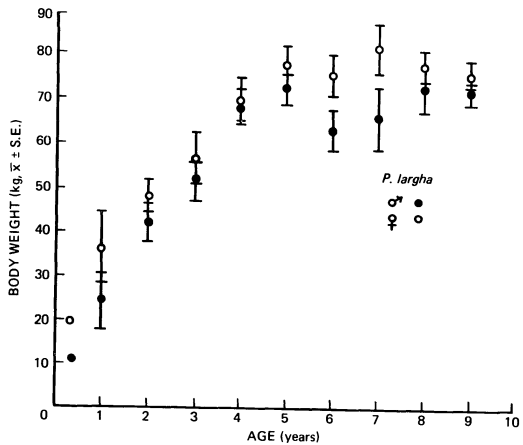


FIGURE 6. Mean annual body weights of two spotted seals from ages 1-9 years. Initial body weights at age 4 months also are indicated.

from 1562 to 2418 cal/g wet weight, representing a lipid content of 5.1 to 18.0%. Pollock samples averaged 1088 cal/g wet weight with 0.8% fat. Protein and ash averaged 19.2% and 1.6%, respectively, in pollock, with a range of 16.3 to 20.0% protein and 2.0 to 2.4% ash in herring samples.

A captive yearling subadult spotted seal and two harbor seals were able to obtain their caloric requirements from herring diets of varying energy content by adjusting their food intake during *ad libitum* feeding. Consumption by captive yearling and subadult seals was highest in winter and lowest in summer, regardless of food energy content. The food consumption of captive spotted seals declined with age from 1 to 9 years according to the equation $y = 12.2(x + 1)^{-0.77}$ ($r = -0.95$).

CHAPTER III

ENERGY ASSIMILATION: APPARENT DIGESTIBLE ENERGY OF FOOD



Introduction

The digestibility of a food or nutrient refers to the proportion absorbed while in transit through the digestive tract, and is equivalent to gross ingested energy minus fecal energy (Schneider and Flatt, 1975). Digestion coefficients are specific for the proximate analysis of the food they represent and cannot be applied to other foods of different nutrient composition (Schneider and Flatt, 1975).

The percent digestibility of foodstuffs is determined by feeding trials with animals, using a direct, total collection method or an indirect, indicator or tracer method. In total collection experiments, weighed portions of feed of known chemical composition and caloric content are fed to animals initially to rid the digestive tract of former food residues and then to maintain stable weight. Feces are collected and weighed over a period of several days, and fecal samples are analyzed chemically. The difference between the amount and chemical composition of food consumed and amount and chemical composition of feces excreted equals that portion which has been apparently digested. Digestibility is apparent because the feces contain residues both of food and of metabolic origin (Crampton and Harris, 1969). Digestible energy (DE) is usually based on the food dry weight because the moisture content of food contributes nothing to the total caloric value. Indicator or tracer digestibility experiments involve the determination of the amount of an indigestible substance in food and feces in addition to chemical analysis of nutrient content. Apparent digestibility is calculated from the ratio of the amount of physiologically inert indicator in a measured

quantity of feces. In this method, only small portions of food and feces need to be weighed and total collection of feces is avoided.

Total collection methods have been used for determination of digestibility in domestic and wild ruminants such as cattle, sheep, and deer (Brody, 1945; Balch, 1950; Smith, 1950; Blaxter and Wainman, 1961; Ullrey, Youatt, Johnson, Fay, Brent, and Kemp, 1968; Ullrey, Youatt, Johnson, Fay, Schoepke, and Magee, 1969; Mautz, 1971; Thompson, Holter, Hayes, Silver, and Urban, 1973), non-ruminant herbivores such as horses (Brody, 1945; Barth, Williams, and Brown, 1977), omnivores such as rodents (Johnson and Groepper, 1970; Smith and Follmer, 1972; Batzli and Cole, 1979), and carnivores such as bobcats (Golley, Petrides, Rauber, and Jenkins, 1965), foxes (Vogtsberger and Barrett, 1973), and weasels (Golley, 1960). Indicators which have been successfully used in the indirect determination of digestibility include chromic oxide or Cr_2O_3 (Crampton and Lloyd, 1951; Czarnocki, Sibbald, and Evans, 1961; Arthur, 1970), lignin (Schneider and Flatt, 1975) chromium-51 as $^{51}\text{Cr}_2\text{O}_3$ (Moore, 1957; Brandt and Thacker, 1958) and as $^{51}\text{CrCl}_3$ (Mautz and Petrides, 1967; Petrides, 1968; Mautz, 1969, 1971), chromogen, and fecal nitrogen (Schneider and Flatt, 1975).

Studies of the digestibility of foods for captive pinnipeds are few, and for wild pinnipeds are nonexistent. Parsons (1977) used the total collection method to determine the digestibility of herring and capelin diets for captive adult ringed seals. Both total collection and $^{51}\text{CrCl}_3$ tracer techniques were used to estimate the digestibility of herring and pollock diets for captive subadult northern fur seals by

Miller (1978) who obtained essentially identical results by both methods. In Miller's study, the digestibility of capelin and squid were determined by total collection of excreta. The results of these investigations are compared to data on the digestibility of different diets for other mammals in Table 6.

Factors affecting the digestibility of foodstuffs include the chemical composition of the food, feeding level or plane of nutrition, and food preparation or processing. The digestibility of nutrients is directly proportional to the percentage of protein in the ration (Schneider and Flatt, 1975). Rats fed diets with increased protein content but equal caloric content had greater digestibility of protein and energy (Brody, 1945). Increased concentrations of fat in a ration increase the digestibility of fat, but decrease the digestibility of other nutrients (Lloyd, McDonald, and Crampton, 1978). The apparent digestibility of a ration decreases as the amount of food fed increases, provided the proportion of nutrients remains constant, while sub-maintenance rations are generally more digestible than higher levels of food intake (Schneider and Flatt, 1975). The higher intake of growing animals exerts only a small depressing effect upon the digestibility of the ration (Schneider and Flatt, 1975). In general, food processing (such as grinding and chopping) does not improve digestibility for growing animals and in some cases may depress it because of more rapid passage of food through the gut (Maynard *et al.*, 1979). Increasing the surface area of a food by grinding or chopping may be beneficial for very young animals before tooth development and in older animals with poor teeth (Schneider and

TABLE 6. The apparent digestibility of different diets in several species of marine and terrestrial mammals.

Species	Diet	Apparent Digestibility (% Gross Energy)	Source
<i>Phoca hispida</i> (Ringed seal)	Herring	96.8	Parsons, 1977
	Capelin	97.8	"
<i>Callorhinus ursinus</i> (Northern fur seal)	Herring	93 (91.4)*	Miller, 1978
	Pollock	90 (86.6)*	"
	Capelin	88	"
	Squid	92	"
<i>Enhydra lutris</i> (Sea otter)	Clams, squid, abalone	82	Costa, in press
<i>Lynx rufus</i> (Bobcat)	Chicken	90	Golley, Petrides,
	Rabbit	90.5	Rauber, and
	Deer	89.5	Jenkins, 1965
<i>Vulpes fulva</i> (Red fox)	Rabbit	91	Vogtsberger and Barrett, 1973
<i>Mustela nivalis</i> (Least weasel)	Voles	89.9	Golley, 1960
<i>Lasiurus cinereus</i> (Hoary bat)	Mealworms	91	Brisbin, 1969
<i>Cryptotis parva</i> (Least shrew)	Mice	90.1	Barrett, 1969
<i>Microtus pennsylvanicus</i> (Meadow vole)	Alfalfa	89.8	Golley, 1960
<i>Microtus californicus</i> (California vole)	Bromegrass	48.8	Batzli and
	Ryegrass seeds	73.0	Cole, 1979
<i>Microtus ochrogaster</i> (Prairie vole)	Alfalfa	65.5	Batzli and
	Bluegrass	49.6	Cole, 1979

TABLE 6. Continued.

Species	Diet	Apparent Digestibility (% Gross Energy)	Source
<i>Lemmus sibericus</i> (Brown lemming)	Tundra grass	35.1	Batzli and Cole, 1979
	Arctic sedge	34	
	Cotton grass	39.3	"
	Mosses	25.4	"
<i>Oryzomys palustris</i> (Rice rat)	Mealworms	94	Sharp, 1967
<i>Odocoileus virginianus</i> (White-tailed deer)	Mixed concentrate	75.5	Thompson, Holter, Hayes, Silver, and Urban, 1973
<i>Rattus norvegicus</i> (Rat)	68% wheat + 7% sucrose + 13% dried skim milk + 11% cream + 1% salt	87	Crampton, and Lloyd, 1951
<i>Cavia porcellus</i> (Guinea pig)	"	83	"
<i>Ovis aries</i> (Sheep)	"	75	"
<i>Sus scrofa</i> (Swine)	"	91	"
<i>Homo sapiens</i> (Human)	"	90	"
<i>Equus equus</i> (Horse)	Hay	59.2	Barth, Williams, and Brown, 1977
	Hay + concentrate	66	
<i>Bos taurus</i> (Steer)	Not given	73	Brody, 1945

*Determined by $^{51}\text{CrCl}_3$ tracer technique.

Flatt, 1975). Cooking does not increase food digestibility in mature farm animals, except for some kinds of foods consumed by swine and poultry (Maynard *et al.*, 1979).

Age, exercise, feeding frequency, and water intake have not been conclusively determined to influence digestibility in most species that have been studied (Mautz, 1971; Schneider and Flatt, 1975). Very young animals may be unable to digest foods completely until their gut is well developed, and the digestive abilities of older animals may be impaired by poor dentition and declining health. The digestibility of foods in young animals may be more affected by parasite infestation of the gut than by other factors (Schneider and Flatt, 1975).

In this study, the apparent digestibility of pollock and herring was determined in two age classes of Bering Sea harbor seals. Food passage rates through the gastrointestinal tracts of the captive seals also were measured and their relationship to digestibility examined.

Methods and Materials

The apparent digestibility of pollock and herring was determined in two 4-year-old harbor seals. Apparent digestibility of herring alone was determined in two yearling harbor seals. Digestibility of pollock was not determined for yearling seals because they refused to eat it. Each feeding trial was conducted during an 8-day period in October and November 1978 using the $^{51}\text{CrCl}_3$ labeling technique (Mautz, 1971; Miller, 1978). The four seals were housed in individual outdoor enclosures 3.6 x 1.5 x 2.4 m with walls of concrete and chain-link fencing and

smooth concrete floors. The seals and their pens were thoroughly hosed with fresh water twice daily, but the seals were denied access to their pools to facilitate sample collection. A 5-day period was permitted for acclimation of the seals to the test conditions. A solution of $^{51}\text{CrCl}_3$ (New England Nuclear) in distilled water at a concentration of 0.6 $\mu\text{Ci}/\text{ml}$ was uniformly injected with a tuberculin syringe (1 cc) and 25-gauge needle into pollock and herring at the level of 1 ml/100 g fish. The fishes were blotted dry with paper toweling and weighed to the nearest 0.5 g on a solution balance (O'Haus Model 1195). Only intact, undamaged fishes were used and an equal number of small injections were made uniformly into the musculature on both sides of each fish. The injected fishes were fed to the seals at maintenance levels (constant body weight); the amounts of pollock and herring offered in each trial were adjusted to maintain caloric equivalence. The seals were fed unlabeled (not injected) fishes for 3 days prior to the start of each experiment to rid each animal's digestive tract of former food residues.

Each seal was given a full day's ration in one feeding by hand; feeding times for each animal were staggered over a 4-hour period to permit ample time for food and sample preparation. Fishes labeled with $^{51}\text{CrCl}_3$ were fed for 7 (pollock) or 8 (herring) consecutive days; thereafter unlabeled fishes were fed at the same maintenance level. Fecal samples, if present, were collected at half-hour intervals for 12 days from each seal. Each fecal sample and fish standard was placed in a tared aluminum pan and oven-dried at 80°C (Costa, in press) for a minimum of 3 days until constant weight was obtained. Each dried

sample and standard was finely ground by means of a mortar and pestle and stored in a vacuum dessicator with CaSO_4 (Hammond Drierite) at room temperature until needed. The mortar and pestle were washed and dried after preparation of each sample to prevent cross-contamination. Three 1-g aliquots (one sub-sample plus two replicates) of each ground fecal sample were weighed to the nearest 0.1 mg on an analytical balance (Mettler Model H20) and placed in each of three 15 x 175 mm glass gamma counting tubes with plastic snap-on caps (Amersham-Searle) in a test-tube rack. Electrostatic attraction between the dry material and tube walls necessitated the addition of 2 ml methanol by eyedropper. A blunt-ended glass rod was used to gently mix the solid material and methanol to eliminate air bubbles and tamp down particles clinging to the tube walls. A few drops of methanol were used to rinse the rod over the tube and the rod was dried for use with the next sample. The tubes were capped and refrigerated overnight at 4°C to permit settling of contents. Once settled, the contents were adjusted to a total height of 3.5 cm with additional methanol (approximately 1.2 cm of solids and the remainder methanol). Three 1.5-g portions of each ground fish standard were prepared in the same manner. The larger amount of fish standard per tube yielded 1.2 cm of solids as settled contents.

Each sample and standard were counted for 10 minutes in a gamma spectrometer (Searle Analytic Automated Gamma System Model 1195), corrected for background radiation; from this the concentration of ^{51}Cr per gram of dry sample was determined. To determine if radioactivity contained in the methanol layer contributed a significant error to the

sample count (because its height above the sample caused it to escape detection by the gamma spectrometer), aliquots of the methanol layer from random fecal samples and fish standards also were counted. The natural logarithm of the ^{51}Cr concentration of each fecal sample was plotted *versus* time after first ingestion of labeled food. Percent apparent digestibility (DE) was calculated for each occurrence of stable fecal isotope excretion according to the equation:

$$\frac{[^{51}\text{Cr}]_{\text{feces}} - [^{51}\text{Cr}]_{\text{food}}}{[^{51}\text{Cr}]_{\text{feces}}} \times 100\% = \text{DE} \quad (4)$$

where $[^{51}\text{Cr}]_{\text{feces}}$ equals the isotope concentration of each fecal sample and $[^{51}\text{Cr}]_{\text{food}}$ equals the isotope concentration of each fish standard. A mean value of percent digestibility was calculated for the entire trial from the individual values of DE. Since the number of seals tested was small and only one trial was performed per seal, each value of DE obtained for individual stable fecal isotope excretions was considered to be a separate statistical event. Means were considered to be significantly different if $P < 0.05$ according to Student's "t" test.

Transit time, or the time required for the passage of the first undigested portion of a meal through the gastrointestinal tract, was determined from the time elapsed between ingestion of the first labeled meal and appearance of the first labeled feces (initial defecation time). The clearance rate, or the time required for excretion of the final fraction of a meal, was obtained by least squares regression analysis of fecal isotope concentration after the first post-test unlabeled fishes

were fed to the seals (Mautz and Petrides, 1971). Gastrointestinal turnover time (GI turnover time), or the time necessary for complete passage of a meal through the digestive system, was estimated from clearance rate. Regression coefficients were tested for significant difference from zero using Student's "t" distribution (Edwards, 1976).

Results and Discussion

Representative patterns of fecal isotope excretion by yearling and 4-year-old harbor seals fed ^{51}Cr -labeled herring and one 4-year-old harbor seal fed ^{51}Cr -labeled pollock are shown in Figures 7, 8, and 9, respectively. As described for other mammals (Mautz, 1971; Mautz and Petrides, 1971), the typical pattern consists of a mixing phase marked by increasing ^{51}Cr concentration, an equilibrium phase characterized by stable isotope excretion, and a declining phase marked by decreasing fecal ^{51}Cr concentration per hour following first feeding of unlabeled food (isotope pool dilution or "washout"). Stable fecal isotope concentration was obtained 12 to 18 hours after first ingestion of labeled herring by all of the seals, and 88 to 112 hours after first ingestion of labeled pollock in two 4-year-old harbor seals. The slower attainment of equilibrium in the pollock trials is attributed to a longer mixing phase, possibly caused by retention of pollock in the gastrointestinal tract of each seal. The declining phase of fecal ^{51}Cr concentration in each seal fed pollock exhibited a segment of rapid decline followed by one that was much slower. This also suggested retention of pollock in some part

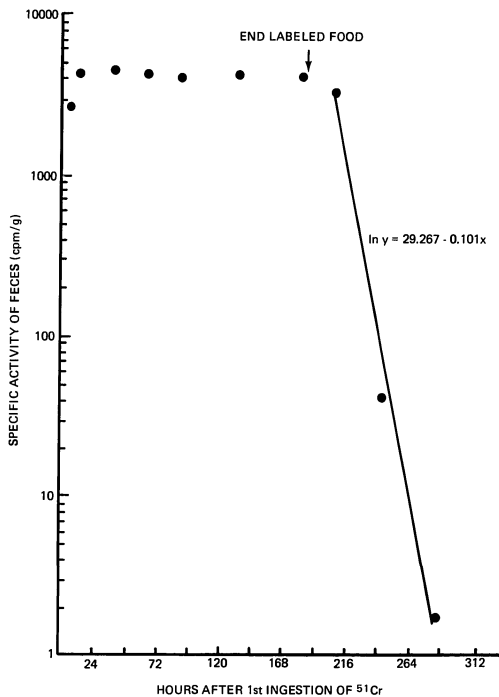


FIGURE 7. Pattern of fecal ^{51}Cr excretion of one yearling harbor seal fed a maintenance ration of herring daily for 8 days.

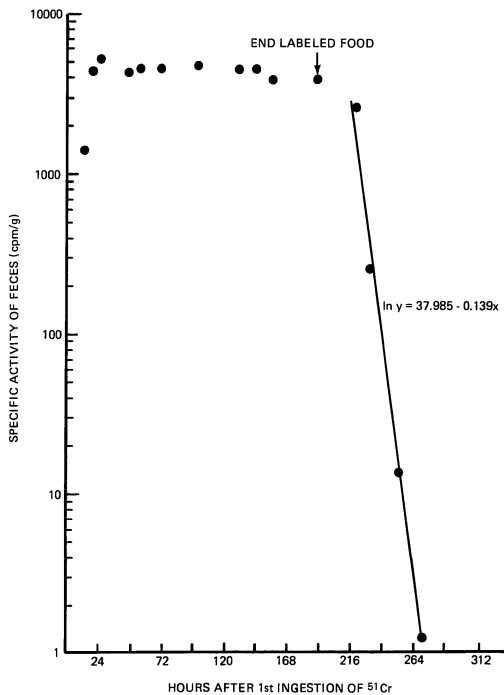


FIGURE 8. Pattern of fecal ^{51}Cr excretion of one 4-year-old harbor seal fed a maintenance ration of herring daily for 8 days.

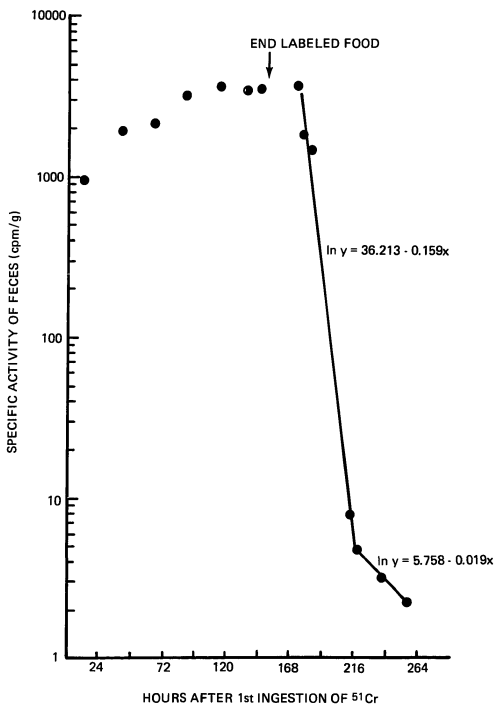


FIGURE 9. Pattern of fecal ^{51}Cr excretion of one 4-year-old harbor seal fed a maintenance ration of pollock daily for 7 days.

of the GI tract, possibly as a result of the greater amount of cartilage contained in these fishes as compared with herring.

In fecal samples and fish standards, the radioactivity of the methanol layer contributed an error of -0.2% to the total count, which was not considered significant.

Table 7 lists values of percent digestibility for pollock and herring diets in harbor seals, compared with results in two other species of pinnipeds. These results indicate that at least 90% of gross food energy is available to pinnipeds as digestible energy, a typical value for mammalian carnivores (Golley, 1960; Golley *et al.*, 1965; Barrett, 1969; Vogtsberger and Barrett, 1973). The digestibility of herring was the same in all the harbor seals tested. However, it was significantly different ($P < 0.001$) from that of pollock in the 4-year-old seals. For each food item, there was no significant difference in digestibility between sexes of seals, although small sample sizes may have precluded the appearance of such differences.

The transit time, clearance rate, and GI turnover time of pollock and herring in harbor seals is presented in Table 8, with comparative data on ringed seals (Parsons, 1977). Great variation between individuals was observed in all food passage rate parameters measured. Transit time, or initial defecation time, tended to be more rapid in seals fed herring than in the same animals fed pollock, although the sample size was too small for statistical comparison. Clearance rate was equivalent to the slope (regression coefficient) or the regression line describing the percent decrease in isotope concentration with time for

TABLE 7. Apparent digestibility of herring and pollock diets for three species of pinnipeds.

Species	Age (yrs)	Food Item	Apparent Digestibility (% Gross Energy) $\bar{x} \pm s.d.$	Source
Pacific harbor seal	1	Herring	90.6±0.7	This study
<i>(Phoca vitulina richardsi)</i>	1	Herring	91.1±0.5	This study
	4	Herring	91.4±0.1	This study
	4	Herring	91.7±0.7	This study
	4	Pollock	96.6±0.2	This study
	4	Pollock	96.8±0.2	This study
Northern fur seal	Subadult	Herring	93.0	Miller, 1978
<i>(Callorhinus ursinus)</i>	Subadult	Herring	93.0	Miller, 1978
	Subadult	Herring	93.0	Miller, 1978
	Subadult	Pollock	90.0	Miller, 1978
Ringed seal	Adult	Herring	96.9	Parsons, 1977
<i>(Phoca hispida)</i>	Adult	Herring	96.2	Parsons, 1977
	Adult	Herring	96.3	Parsons, 1977
	Adult	Herring	97.9	Parsons, 1977

TABLE 8. Food transit time, clearance rate, and gastrointestinal turnover time measured in captive pinnipeds.

Species	Age (yrs)	Sex	Body Wt. (kg)	Diet & Daily Intake (kg)	Transit Time (hrs)	% Clearance Rate (hr^{-1})	GI Turnover Time (hrs)	Source
Harbor seal (<i>Phoca vitulina richardsi</i>)	4	♂	44.1	Herring: 2.2	9.6	12.5	8.0	This study
	4	♀	45.2	Herring: 1.8	10.5	13.9	7.2	This study
	1	♂	31.8	Herring: 1.6	7.8	10.1	9.9	This study
	1	♀	31.8	Herring: 1.7	8.6	15.7	6.4	This study
	4	♂	45.4	Pollock: 3.3	12.3	14.1, 2.5	7.1, 40.0	This study
	4	♀	48.6	Pollock: 2.9	11.5	15.9, 1.9	6.3, 52.6	This study
Ringed seal (<i>Phoca hispida</i>)	Adult	♀	30-32.5	Herring: --	5.75± 0.65	--	--	Parsons, 1977
	Adult	♂	45-55.0	Herring: --	16.41±21.15	--	--	Parsons, 1977
	Adult	♀	38-41.0	Herring: --	8.45± 4.45	--	--	Parsons, 1977
	Adult	♀	40-43.0	Herring: --	5.80± 2.36	--	--	Parsons, 1977
	Adult	♂	77-80.5	Herring: --	7.76± 1.80	--	--	Parsons, 1977

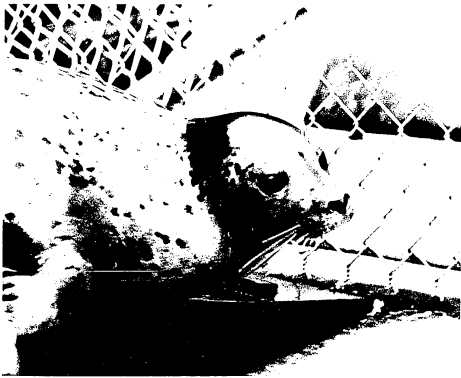
each seal tested. The slope of each regression line was significantly different from zero ($P < 0.01$). No significant difference was observed between clearance rate (or GI turnover time) and food intake. The slower clearance rate (and turnover time) of the latter segment of the two-part declining phase of fecal isotope excretion observed in seals fed pollock may partially account for the higher digestibility of this food in the seals tested.

Summary

Captive Bering Sea harbor seals were able to digest about 91% of the gross energy of a herring diet and about 97% of a pollock diet. The transit times, clearance rates, and GI turnover times measured for herring and pollock in harbor seals reflect a more rapid passage of digesta through the gut of these pinnipeds than other large carnivores. A two-phase system of fecal isotope excretion was observed in harbor seals fed pollock, consisting of a rapid rate of isotope clearance followed by a much slower clearance rate. This may partially explain the higher digestibility of pollock as compared with herring in the seals tested. Preliminary studies indicate that the high digestibility coefficients seem not to vary with age or sex of the seals.

CHAPTER IV

ENERGY ASSIMILATION: METABOLIZABLE ENERGY AND SPECIFIC DYNAMIC
ACTION OF FOOD



Introduction

Metabolizable energy (ME) is estimated as the difference between apparent digestible energy and the energy contained in urine and in the gaseous products of digestion (Maynard *et al.*, 1979). Urinary energy loss results from the excretion of incompletely oxidized nitrogenous products, principally urea in mammals, which are of exogenous (food) and endogenous (metabolic) origin. On a nitrogen-free diet or during fasting, the endogenous urinary nitrogen represents the total nitrogenous excretion (Maynard *et al.*, 1979). Gaseous energy losses are of great importance in the energy budgets of ruminants, but are negligible in monogastric mammals. These gases consist primarily of methane, with traces of hydrogen and hydrogen sulfide (Schneider and Flatt, 1975).

Nitrogen-corrected metabolizable energy (ME_n) may be calculated for situations where body protein is gained (positive nitrogen balance during growth) or lost (negative nitrogen balance during starvation or old age) from Rubner correction factors (Brody, 1945; Maynard *et al.*, 1979). During positive nitrogen balance, 7.45 kcal/g of nitrogen stored is added to the urinary energy, resulting in a lower value of ME. During negative nitrogen balance, 7.45 kcal/g of nitrogen lost is subtracted from the urinary energy, causing an increase in ME. This represents a more exact determination of metabolizable energy.

The increase in metabolic rate of a resting, previously unfed animal after ingestion of food is the "specific dynamic action (SDA)" (Rubner, 1902), "calorigenic effect" (Kleiber, 1975) of food, or "heat increment of feeding (HI)" (Maynard *et al.*, 1979). The SDA or HI

consists of the "heat of fermentation (HF)," resulting from microbial action in the gut, and the "heat of nutrient metabolism." HF contributes a great fraction to the total heat increment in ruminants, but is insignificant in monogastric species except herbivores such as horses where considerable fermentation occurs in the cecum and large intestine (Church and Pond, 1974).

SDA is dependent on the amount of food consumed by an animal and its nutrient composition (Hoch, 1971). In terms of the energy content of the food ingested, SDA in a mature dog is about 6% for sucrose, 15% for lipids, and 40% for proteins (Brody, 1945). In the mammals that have been examined, carbohydrates increased basal metabolism by 4 to 30% for 2 to 5 hours after ingestion, lipids from 4 to 15% for 7 to 9 hours, and proteins 30 to 70% for as long as 12 hours (Hoch, 1971). Mixed diets of protein, fat, and carbohydrate result in lower SDA values than those predicted from the individual components (Forbes and Swift, 1944). Elevation of metabolic rate has been correlated with an increase in urinary nitrogen after amino acid intake, suggesting that deamination and urea formation may partly account for the SDA (Buttery and Annison, 1973). SDA also is the result of heat production from the work of mastication, excretion by the kidneys, and increased muscular activity of the gastrointestinal tract and respiratory and circulatory systems associated with nutrient metabolism (Church and Pond, 1974).

The SDA per unit food, particularly protein, will vary with the amount of nutrient taken and with the age and condition of the animal. Increased levels of food intake generally result in an elevated SDA.

Growing, non-lactating, and underfed animals exhibit lower SDA values than older, lactating, or healthier animals on the same diet because the nutrients are largely stored and not catabolized (Brody, 1945).

It has been hypothesized that, in many mammals exposed to cold temperatures, SDA apparently substitutes for the heat of chemical thermoregulation, sparing body fuel reserves and appearing as a decreased SDA (Brody, 1945). Above the thermoneutral zone, SDA adds to heat stress and requires additional energy expenditure to dissipate it (Church and Pond, 1974).

In this study, the metabolizable energy (nitrogen-corrected) and specific dynamic action of pollock and herring diets for Bering Sea harbor seals were obtained from measurements of digestibility, urinary energy, and post-prandial heat production in captive harbor seals. These estimates were used to assess the net energy requirements of several age classes of captive seals. For each seal, digestibility as determined by the $^{51}\text{CrCl}_3$ technique was validated by collecting all feces produced during nitrogen balance tests and comparing fecal energy with ingested energy.

Methods and Materials

Nitrogen Balance Studies

The nitrogen balances of yearling and 4-year-old harbor seals fed herring (2143 ± 75 cal/g wet weight) and of 4-year-old harbor seals fed pollock (1088 ± 59 cal/g wet weight) were determined during separate, 5-day feeding trials conducted immediately after completion of

isotope-tracer digestibility studies with the same animals. Each yearling seal was placed in a 1.00 x 0.75 x 0.65 m stainless steel metabolism cage (Hoeltge Inc., Cincinnati, Ohio) with a removable tray inclined from back to front for collection of feces and urine. Urine was collected under mineral oil (to retard evaporation) in a graduated glass container placed beneath a drain at the front of the tray. Each of the larger, 4-year-old seals was placed in a collapsible metal cage 1.04 x 0.65 x 0.74 m with a bottom mesh of 5.6 x 8.75 cm. The cage was supported on concrete blocks 0.5 m above ground level. A collection tray, made of 18-gauge 1.5 x 0.7 m galvanized sheet steel bent to form a 15° slope from back to front and provided with a drain, was suspended with wire hooks from the underside of the cage. Feces and urine were collected in the same manner as for yearling seals. Seals were hand-fed pollock and herring once per day in measured amounts at maintenance levels (constant body weight) following the routine established in the digestibility trials. Collection trays were checked hourly to avoid contamination of urine by feces. Fresh feces were placed in tared aluminum pans and weighed to the nearest 0.5 g on a solution balance (O'Haus Model 1195). The volume of urine collected in the graduated container was recorded to the nearest milliliter, and the urine was stored in a 500-ml polypropylene, screw-capped bottle (Sybron-Nalge) at 4°C. All urine samples collected during a 24-hour period from a given seal were combined and stored in the same 500-ml bottle. The total urine collected per seal per 24 hours was thoroughly mixed by stirring, and a 100-ml aliquot was placed in a tared 250-ml polypropylene,

screw-capped bottle (Sybron-Nalge) and weighed to the nearest 0.5 g. Fecal and urine samples were frozen at -50°C and then freeze-dried according to the method of Horwitz (1970). Moisture content was obtained as the difference between wet and dry weight of each sample. Each freeze-dried urine sample was homogenized with a mortar and pestle and stored in an aluminum pan in a vacuum dessicator with CaSO_4 (Hammond Drierite) at room temperature until analyzed. Each freeze-dried fecal sample from the same 24-hour period was prepared and stored in the same manner as the urine samples. The nitrogen content of five 15-mg dehydrated samples of feces and five 5-mg samples of urine from each 24-hour period was determined with an automated nitrogen analyzer of $\pm 0.2\%$ accuracy (Coleman Model 29B, Coleman Instruments Division, Perkin-Elmer Corporation) according to the Dumas method (Horwitz, 1970). The nitrogen content of each sample was expressed as percentage wet weight of the original sample. The gross energy content (in cal/g) of each 24-hour collection of feces and urine was determined by combustion of five 1-g samples in a bomb calorimeter (Parr Series 1200 Adiabatic Calorimeter) according to the techniques of Schneider and Flatt (1975). The mean 24-hour nitrogen balance (NB) in grams of each seal was determined according to the equation:

$$\text{NB} = \text{NI} - \text{FN} - \text{UN} \quad (5)$$

where NI equals nitrogen intake (g), FN equals fecal nitrogen (g), and UN equals urinary nitrogen (g). Nitrogen-corrected metabolizable energy (ME_n) in kcal was estimated from the apparent digestible energy and nitrogen balance generated, using the equation:

$$ME_n = (GE - FE - UE) \pm (NB \times 7.45) \quad (6)$$

or

$$ME_n = (DE - UE) \pm (NB \times 7.45) \quad (7)$$

where DE equals digestible energy (kcal), FE equals fecal energy (kcal), UE equals urinary energy (kcal), NB equals nitrogen balance (g), and 7.45 equals the Rubner correction factor (kcal/g). Means were considered to be significantly different if $P < 0.05$ according to Student's "t" test.

SDA Determinations

Specific dynamic action (SDA) of different quantities of herring fed to four yearling harbor seals was estimated from measurements of oxygen consumption in air at thermoneutral conditions in an open-flow system (Figure 10). The animals used in these experiments were thoroughly acclimated to test conditions by previous exposure to the chamber, and they frequently slept during metabolic experiments. Experiments were conducted during 4 days in September 1978 from 0800-2200 ADST in temperature-controlled rooms at 0°C ($\pm 1^\circ\text{C}$) at the Institute of Arctic Biology Animal Facility, Fairbanks. Each day, one seal in a postabsorptive state (12 to 20 hours after feeding) was removed from its pool and allowed to dry completely before tests in air to minimize evaporative heat loss. In the temperature-controlled room, the seal was placed in an aluminum chamber 0.9 x 0.5 x 0.5 m fitted with a clear plexiglass lid which permitted observation. Air was circulated through the chamber by means of a large vacuum pump, and passed through CaSO_4 (Hammond

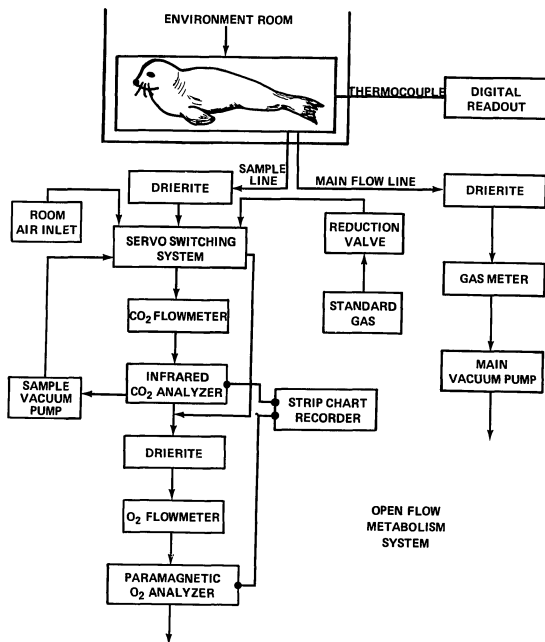


FIGURE 10. Open-flow respirometry system used in metabolic tests with harbor and spotted seals.

Drierite) to remove moisture before entering a dry gas meter (Singer, American Meter Division, Model DTM-200). Flowrates of 45 l/min were required for seals ranging in weight from 25 to 32 kg to maintain carbon dioxide levels below 1%. Flows were calibrated with a Scholander bag spirometer (Scholander and Jensen, 1958). Sample flow, measured by calibrated rotameters (Gilmont), was provided by a small vacuum pump which removed chamber air at a rate of 500 ml/min, passed it through CaSO_4 before circulating it to a carbon dioxide analyzer (Beckman Infrared Model 864), and then passed it to an oxygen analyzer (Beckman Paramagnetic Model F3) at a reduced flow of 150 ml/min. Both analyzers were calibrated with outside air and a standard gas analyzed with a Scholander 0.5 cc Gas Analyzer (Scholander, 1947). Continuous output of both analyzers was provided by a strip-chart recorder (Hewlett-Packard Model 7100B). Recordings were begun 1 hour after the animal was placed in the chamber to allow establishment of a thermal steady-state. Chamber air temperatures were measured by calibrated copper-constantan thermocouples, with all readings displayed on a digital readout thermometer (Fluke Model 2100A). The time required for 95% equilibration of the metabolism chamber to a change in oxygen consumption, as predicted by the equation of Silver (1946), was calculated to be 15 minutes at a flowrate of 45 l/min. The actual time required for a 95% response to a change in oxygen consumption was less than 5 minutes, based on the time necessary to obtain steady-state fractional oxygen concentration on the recorded output of the oxygen analyzer. This reduction in equilibration time was partially attributed to the reduction in total chamber

air volume caused by the presence of the seal itself. After measurement of steady-state oxygen consumption for a minimum of 3 hours, sample and chamber air flows were momentarily disconnected from the chamber and the lid removed to permit *in situ* feeding of a measured portion of whole herring (12% fat, 2143 cal/g wet weight) to the seal. Feeding was accomplished in about 5 minutes, whereupon the lid was replaced and all air flows reconnected. After 15 minutes, recordings were resumed and continued for a maximum of 12 hours postprandial. The seal's total behavioral repertoire was continually monitored throughout the experiment and correlated with record tracings whenever possible. Oxygen consumption (in all tests) and carbon dioxide production (in half of the tests) were calculated for periods of stable respiratory exchange by computing the mean volume fractional concentration of each gas in expired air as a line of best fit for the record tracing obtained during the time interval (see Figure 11). During apneustic periods associated with sleep, which often resulted in record tracings extending nearly full-scale, a planimeter was used to integrate the area beneath the tracing for computation of a mean value over time. The rate of oxygen consumption and carbon dioxide production was then calculated according to the equation of Depocas and Hart (1957), where dry outlet air flow is measured without absorption of carbon dioxide:

$$\dot{V}_{O_2} = \dot{V}_{ESTPD} (F_{I_{O_2}} - F_{E_{O_2}}) \left[\frac{1 - F_{E_{O_2}} - F_{E_{CO_2}}}{1 - F_{I_{O_2}} - F_{I_{CO_2}}} \right] \quad (8)$$

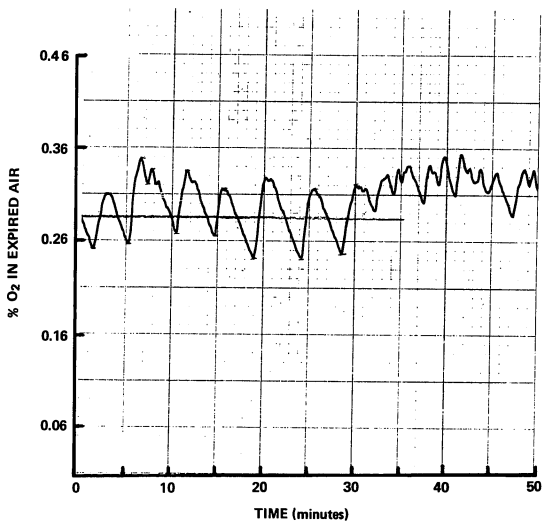


FIGURE 11. Record tracing obtained for sleeping (0-30 minutes) and resting (30-50 minutes) seal during measurement of oxygen consumption with open-flow respirometry.

$$\dot{V}_{CO_2} = \dot{V}_{E_{STPD}} (F_{E_{CO_2}} - F_{I_{CO_2}}) \left[\frac{1 - F_{E_{O_2}} - F_{E_{CO_2}}}{1 - F_{I_{O_2}} - F_{I_{CO_2}}} \right] \quad (9)$$

- \dot{V}_{CO_2} = rate of oxygen consumption in l/min
 $\dot{V}_{E_{STPD}}$ = flowrate of dry outlet air corrected to standard temperature and pressure
 $F_{I_{O_2}}$ = volume fractional concentration of oxygen in inlet air (0.2093)
 $F_{E_{O_2}}$ = volume fractional concentration of oxygen in outlet air (calculated from record)
 \dot{V}_{CO_2} = rate of carbon dioxide production in l/min
 $F_{I_{CO_2}}$ = volume fractional concentration of carbon dioxide in inlet air (0.0003)
 $F_{E_{CO_2}}$ = volume fractional concentration of carbon dioxide in outlet air (calculated from record)

The expression $(1 - F_{E_{O_2}} - F_{E_{CO_2}}) / (1 - F_{I_{O_2}} - F_{I_{CO_2}})$ represents the difference in volume between inlet air and outlet air and is a correction factor for $\dot{V}_{E_{STPD}}$. In tests where only oxygen consumption was measured, this factor was neglected because carbon dioxide levels were maintained below 1% with high flowrates of outlet air. A maximum error of +2.3% in \dot{V}_{O_2} was obtained at a carbon dioxide concentration of 1%.

The respiratory exchange ratio or respiratory quotient (RQ) also was determined for tests where \dot{V}_{O_2} and \dot{V}_{CO_2} were measured:

$$RQ = \frac{\dot{V}_{CO_2}}{\dot{V}_{O_2}} \quad (10)$$

The percentage increase in post-prandial oxygen consumption over pre-prandial levels was calculated by comparing oxygen consumption integrated over time intervals equivalent in duration and behavior for both conditions. Oxygen consumption values were expressed in terms of energy metabolism with use of the caloric equivalent of oxygen appropriate for the measured RQ. Net energy requirements (NE) were estimated as the difference between nitrogen-corrected metabolizable energy (ME_n) and specific dynamic action (SDA) for each diet in all seals tested.

Results and Discussion

Total collection of feces for nitrogen balance studies permitted validation of digestibility trials with $^{51}\text{CrCl}_3$ for each diet in the same animals. Digestibility based on total dry food intake and total output of dry feces, or

$$\frac{\text{Total Food Energy} - \text{Total Fecal Energy}}{\text{Total Fecal Energy}} \times 100\% = \text{DE} \quad (11)$$

differed from digestibility as determined by the concentration of ^{51}Cr in food and feces by $\pm 0.9\%$; this difference was not significant.

The mean daily production and energy content of feces and urine from yearling harbor seals fed herring, and 4-year-old harbor seals fed herring and pollock, are presented in Table 9. The quantity of feces produced and the fecal energy each were inversely proportional to the apparent digestibility of the diet in the 4-year-old seals, while urine production in these animals was slightly higher and more concentrated on a pollock diet. Fecal energy was significantly greater for seals on

TABLE 9. Mean daily production and energy content of feces and urine from harbor seals fed maintenance levels of herring and pollock.

Age (yrs)	Diet & Amount Fed (g dry)	Daily Feces Production (g dry) (g wet)		Daily Urine Production (g dry) (g wet)		Fecal Energy (cal g ⁻¹ dry)	$\bar{x} \pm$ s.d. (cal g ⁻¹ wet)	Urinary Energy (cal g ⁻¹ dry)	$\bar{x} \pm$ s.d. (cal g ⁻¹ wet)
1	Herring 540.7	94.4	325.5	40.0	348.3	2944± 32	854±13	2422± 62	278±2
4	Herring 670.0	122.7	382.2	83.2	773.1	3122±152	1002±51	2400± 81	259±1
4	Pollock 665.0	42.3	129.3	104.4	783.5	2027±123	663±54	2635±150	350±4

a herring diet than for the same animals on a pollock diet ($P < 0.001$), probably reflecting the lower energy content and greater digestibility of pollock.

Nitrogen balances for both age classes of harbor seals fed maintenance rations of herring and pollock are given in Table 10. Values of fecal output calculated as the difference between gross ingested energy and digestible energy (determined by the $^{51}\text{CrCl}_3$ technique) are included with measured fecal output for comparison. The estimated fecal output yielded a nitrogen balance identical to that computed from measured feces production in each animal. All seals exhibited a positive nitrogen balance or nitrogen retention, indicating daily growth or protein gain. On a herring diet, nitrogen retention in yearling and 4-year-old seals was $82.3 \pm 0\%$ and $76.2 \pm 0.2\%$, respectively, of the dietary nitrogen intake. Nitrogen retention in the 4-year-old seals was significantly greater ($P < 0.05$) on a pollock diet ($80.9 \pm 0.2\%$ of dietary intake) than on a herring diet ($76.2 \pm 0.2\%$ of dietary intake), reflecting both the differences in digestibility of protein and the protein content of these foods.

The effect of food quantity (plane of nutrition) and sleep on the magnitude and duration of post-prandial metabolic rate (SDA) in yearling harbor seals is illustrated by Figure 12. In general, the magnitude and duration of SDA varied directly with increasing quantities of herring fed, although sleep tended to depress the overall metabolism (Benedict, 1938; Hoch, 1971; Swan, 1974). In the only SDA test in which a seal remained resting and awake, the measured SDA of 28.2% BMR for 10 hours

TABLE 10. Results of nitrogen balance studies conducted over a 5-day period in two age classes of harbor seals fed maintenance rations of herring and pollock. Values in parentheses are calculated from feces output estimated during $^{51}\text{CrCl}_3$ digestibility trials. Values expressed as \bar{x} .

Age (yrs)	Wt (kg)	Diet/Amount Fed (g dry/kg-day)	Nitrogen Intake (\bar{x}) (g dry/kg-day)	Feces Output (g dry/kg-day)	Fecal Nitrogen (\bar{x}) (g dry/kg-day)	Urine Output (g dry/kg-day)	Urinary Nitrogen (\bar{x}) (g dry/kg-day)	Nitrogen Balance (g dry/kg-day)				
1.0	31.8	Herring	17.0	2.9	0.51	3.0 (3.1)	1.5	0.05 (0.05)	1.2	3.0	0.04	0.42 (0.42)
4.0	45.9	Herring	14.6	2.9	0.42	2.7 (2.5)	1.7	0.04 (0.04)	1.8	3.6	0.06	0.32 (0.32)
4.0	47.6	Pollock	14.0	3.0	0.42	0.9 (1.2)	1.0	0.01 (0.01)	2.2	3.4	0.07	0.34 (0.34)

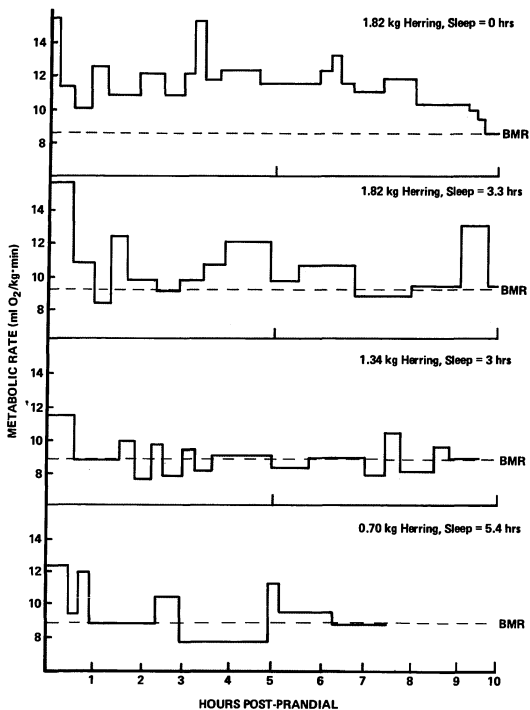


FIGURE 12. The effect of food quantity (herring) and sleep on the magnitude and duration of postprandial metabolic rate in four yearling harbor seals.

was in close agreement with 30.9% BMR for 12 to 13 hours obtained for adult ringed seals on a herring diet (Parsons, 1977) and 30% BMR for dogs on a raw meat diet (Brody, 1945; Hoch, 1971; Kleiber, 1975). Since the percent elevation of BMR by SDA also is dependent on the size of the animal, SDA is better expressed in terms of the energy content of the food ingested (Kleiber, 1975; Bartholomew, 1977). The measured 28.2% elevation in basal metabolism corresponds to a value of 177 kcal for the 10-hour period, which is equivalent to approximately 5.5% of the metabolizable energy and 4.7% of the gross energy of the food ingested by the seal. As the number and duration of sleep episodes increased, metabolism was depressed to the extent that a smaller ration fed to an awake seal had a greater SDA than a larger ration fed to an animal which slept a great deal. Lacking data for SDA of different diets and food rations larger than maintenance levels in additional seals, 292.9 cal/g dry food (derived from the dry weight of herring and corresponding increase in metabolism over basal) was assumed to be a reasonable estimate of SDA for yearling and 4-year-old harbor seals fed herring or pollock.

Table 11 lists energy budget components UE (urinary energy), FE (fecal energy), ME (metabolizable energy), ME_n (nitrogen-corrected metabolizable energy), SDA (specific dynamic action), and NE (net energy) for seals in this study and others. Fecal and metabolizable energy for harbor seals were derived from digestible energy values measured by the $^{51}\text{CrCl}_3$ method. Fecal energy was estimated as the difference between gross ingested energy and digestible energy, with back-calculation of

TABLE 11. Estimates of energy budget components FE (fecal energy), UE (urinary energy), ME (metabolizable energy), ME_N (nitrogen-corrected metabolizable energy), SDA (specific dynamic action), and NE (net energy) for pinnipeds fed herring and pollock.

Species	Age (yrs)	Wt (kg)	Daily Food Intake (g dry wt)	Daily Feces Production (g dry wt)	Daily Urine Production (g dry wt)	Energy Budget Components (% GE)						Reference
						FE	UE	ME	ME _N	SDA	NE	
Pacific harbor seal	1	31.8	Herring 540.7	100.1 (calc)	40.0 (meas)	8.8	2.9	88.3	85.3	4.7	80.6	This study
	4	44.6	Herring 670.0	116.9 (calc)	83.2 (meas)	8.8	4.8	86.4	83.7	4.7	80.0	This study
	4	47.6	Pollock 665.0	55.6 (calc)	104.4 (meas)	3.3	7.3	89.4	85.9	5.7	80.2	This study
Northern fur seal	Subadult	15-30	Herring 472.8	33.5	44.0	3.2	3.2	89.8	--	--	--	Hiller, 1978
	Subadult	26.8	Pollock 632.7	63.2	44.0	3.3	2.5	87.5	--	--	--	Hiller, 1976
Ringed seal	Adult	31.2	Herring	--	--	3.1	9.8	87.1	--	--	--	Parsons, 1977
	Adult	39.5	Herring	--	--	3.8	9.0	87.2	--	--	--	Parsons, 1977
	Adult	29.5	Herring	--	--	3.7	10.2	86.1	--	--	--	Parsons, 1977
	Adult	78.7	Herring	--	--	2.7	5.4	92.5	--	--	--	Parsons, 1977

fecal production from the known caloric value of dry feces. Metabolizable energy was estimated as the difference between digestible energy and the combined energy of feces and urine. Values of ME for all pinnipeds studied ranged from 86.1 to 92.5% of gross energy, reflecting the high digestibility of herring and pollock diets in these species. Values of ME for two age classes of harbor seals varied according to the protein status of each animal, indicated by the nitrogen balance for each diet. The harbor seals examined were still growing, retaining nitrogen for use in new tissue production and tissue replacement. The difference in ME decreased after application of a correction factor for nitrogen retention to these values (calculation of ME_n). The net energy, in terms of percent gross energy available from herring fed to yearling seals and from herring and pollock fed to 4-year-old seals, was nearly identical; the mean of these values, 80.3% GE, was assumed to be a reasonable estimate of the net energy required by harbor and spotted seals fed herring (12.2% fat) or pollock (0.8% fat).

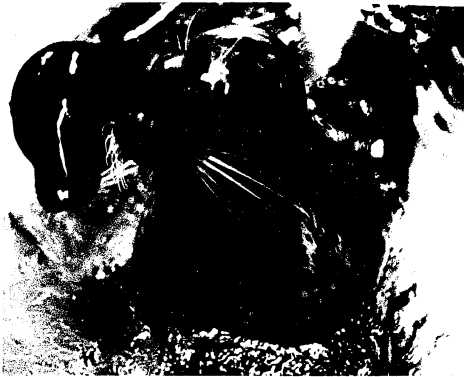
Summary

More nitrogen per kilogram of body weight was retained by captive yearling Bering Sea harbor seals fed herring than by subadult harbor seals fed herring or pollock. This is characteristic of young, growing mammals undergoing rapid tissue production and replacement. The significantly higher nitrogen retention generated by a pollock diet than by a herring diet in subadult harbor seals was a consequence of the greater quantity and digestibility of protein in pollock. Nitrogen-corrected metabolizable

energy (ME_n) for yearling and subadult seals fed maintenance rations of herring was estimated at 85.3% and 83.7% of gross ingested energy (GE), respectively. Adult seals fed maintenance rations of pollock had an estimated ME_n value of 85.9% GE because of greater nitrogen retention. The specific dynamic action (SDA) of herring fed at maintenance levels to yearling harbor seals was 5.5% ME, or 4.7% GE, corresponding to an average increase in metabolism of 28.2% over basal that lasted approximately 10 hours. The magnitude and duration of SDA rose with increased quantities of herring fed and was diminished by sleep. Values of 292.9 cal/g dry food and 80.3% of gross energy were assumed to be reasonable estimates of the SDA and net energy (NE) components, respectively, of the energy budgets of harbor and spotted seals fed herring or pollock.

CHAPTER V

ENERGY UTILIZATION: ESTIMATION OF NET ENERGY FOR MAINTENANCE



Introduction

That part of the net ingested energy available to a mammal for basal metabolism, activity, sleep, and thermoregulation is termed maintenance energy (NE_m). In pinnipeds, maintenance energy requirements from resting and active states at different temperatures have been estimated primarily from determinations of metabolic rate by oxygen consumption experiments.

Resting and Basal Metabolism

Most measurements of resting metabolic rate in pinnipeds have yielded values greater than those predicted by Kleiber's (1975) equation for terrestrial mammals which relates daily metabolic rate in kilocalories (or standard metabolic rate) to 70 times the $3/4$ power of body weight in kilograms ($M = 70W^{3/4}$). As in growing terrestrial mammals (Kleiber, 1975), newborn and young seals exhibited higher resting metabolic rates than adults. Values observed in newborn and pre-nursing Weddell seals (Elsner, Hammond, Denison, and Wyburn, 1977) and harp seals (Davydov and Makarova, 1964), were more than four times those predicted for terrestrial mammals of the same weight; for harbor and elephant seals several days to several months old the values were 1.5 to 2.3 times predicted levels (Scholander, 1940; Irving and Hart, 1957; Hart and Irving, 1959; Miller and Irving, 1975; Miller, Rosenmann, and Morrison, 1976; Elsner *et al.*, 1977; Heath, McGinnis, and Alcorn, 1977; Ortiz, Costa, and LeBoeuf, 1978; Costa and Ortiz, 1980). Elevated rates of resting metabolism have been reported in subadult California sea lions

(Matsuura and Whittow, 1973), subadult northern fur seals (Iversen and Krog, 1973; Ohata, 1976; Miller, 1978), subadult harbor seals (Craig and Päsche, 1980), and adult Weddell seals (Kooyman, Kerem, Campbell, and Wright, 1973; Kooyman, 1975). Rates approaching Kleiber's (1975) values for terrestrial mammals have been obtained for an adult harbor seal (Matsuura and Whittow, 1973), freely diving adult harp seals (Øritsland and Ronald, 1975; Gallivan, 1977; Gallivan and Ronald, 1979), and adult ringed seals (Parsons, 1977). An apparent decrease in metabolic rate with increasing age and size has been noted in harp seals; the highest rates always occurred in lean animals (Øritsland and Ronald, 1975).

A comprehensive listing of reported values for resting metabolism in 13 species of pinnipeds is presented in Table 12. Only seven values have been reported as basal metabolic rates (Miller and Irving, 1975; Miller *et al.*, 1976; Ohata, 1976; Miller, 1978), the remainder having been measured under conditions other than the rigorous criteria established for BMR determinations (Benedict, 1938; Hoch, 1971; Bartholomew, 1977; Bray and Atkinson, 1977). Pierce's (1970) measurement of metabolic rate in a young harbor seal included activity increments from sustained swimming and diving. The forced restraint of seals in several experiments may have resulted in elevated resting rates (Irving, Solandt, Solandt, and Fisher, 1935; Scholander, 1940; Scholander, Irving, and Grinnell, 1942b), although in some cases the animals were reported to be relaxed and quiet, yielding reproducible results (Irving and Hart, 1957; Hart and Irving, 1959). The results of Craig and Päsche (1980) were obtained from seals that were sedated and not in postabsorptive

TABLE 12. Resting metabolic rates

Species	Age
<i>Phoca vitulina</i> spp.	Young
	Young
	2 yrs.
<i>Phoca vitulina concolor</i>	4-8 mos.
	4-8 mos.
<i>Phoca vitulina vitulina</i>	Young
<i>Phoca vitulina richardsi</i>	1-2 wks.
	< 5 wks.
	3-5 mos.
	Young
	> 10 yrs.
<i>Phoca largha</i>	Pup
	1 yr.

measured in 13 species of pinnipeds.

Wt (kg)	Metabolic Rate		watts/kg	Source
	ml O ₂ /kg·min	kcal/day		
29	9.1	1805 (875)*	3.0	Irving, Solandt, Solandt, and Fisher, 1935
20	10.0	1368 (662)	3.3	Scholander, Irving, and Grinnel, 1942b
42.5	6.1	1773 (1165)	2.0	Craig and Päsche, 1980
26-41	8.3	1902 (975)	2.7	Irving and Hart, 1957
23-33	8.0	1522 (852)	2.6	Hart and Irving, 1959
20	9.9	1354 (663)	3.3	Harrison and Kooyman, 1968
12-15	12.3	1136 (493)	4.1	Miller, Rosenmann, and Morrison, 1976
10-13	13.3	1046 (437)	4.4	Miller and Irving, 1975
18-27	8.3	1277 (723)	2.7	Miller and Irving, 1975
39	6.0	1605 (1094)	2.0	Pierce, 1970
98	3.8	2547 (2180)	1.2	Matsuura and Whittow, 1973
19	4.8	600 (623)	1.5	Iversen and Krog, 1973
35.5	5.7	1384 (1018)	1.9	Hammel, Elsner, Heller, Naggert, and Bainton, 1977

TABLE 12. Continued.

Species	Age	Wt (kg)	Metabolic Rate			Source
			ml O ₂ /kg·min	kcal/day	watts/kg	
<i>Phoca groenlandica</i>	< 7 da.	7-12	17.5	1365 (434)	6.9	Davydov and Makarova, 1964
	8-15 da.	15-25	15.8	2172 (664)	5.3	Davydov and Makarova, 1964
	Pup	17.5	7.3	878 (599)	2.4	Iversen and Krog, 1973
	Weaned	30-34	11.9	2946 (1033)	4.5	Davydov and Makarova, 1964
	30-40 da.	31.6	7.4	1599 (933)	2.4	Davydov and Makarova, 1964
	Young	35-42	6.4	1686 (976)	2.1	Irving and Hart, 1957
	1 yr.	40	4.1	2000 (1122)	2.4	Wekstein and Krog, 1971
	6 yrs.	108-160	2.9	2807 (2852)	1.0	Gallivan and Ronald, 1979
<i>Phoca hispida</i>	Adult	130	2.9	2579 (2695)	1.0	Øritsland and Ronald, 1975
	Adult	37	3.1	778 (1051)	1.0	Parsons, 1977
<i>Leptonychotes weddellii</i>	Adult	72	2.2	1104 (1729)	0.7	Parsons, 1977
	Newborn	25	21.2	3625 (783)	7.0	Elsner, Hammond, Dension, and Wyburn, 1977
	Nursing	26	9.6	1707 (806)	3.2	Elsner <i>et al.</i> , 1977
<i>Halichoerus grypus</i>	Adult	425	5.1	14826 (6839)	1.7	Kooyman, Kerem, Campbell, and Wright, 1973
	Young	48	5.9	1950 (1276)	2.0	Scholander, 1940
<i>Cytophoca cristata</i>	Young	29	8.6	1706 (875)	2.8	Scholander, 1940

TABLE 12. Continued.

Species	Age	Wt (kg)	Metabolic Rate			Source	
			ml O ₂	kg·min	kcal/day		watts/kg
<i>Histiophoca fasciata</i>	Young	47-61	6.8		2512 (1394)	2.2	Iversen and Krog, 1973
<i>Callorhinus ursinus</i>	Subadult	32	7.7		1685 (942)	2.5	Iversen and Krog, 1973
	2-6 yrs.	15-28	8.3		1225 (699)	2.8	Ohata, 1976
	2-5 yrs.	21	9.7		1393 (687)	3.2	Miller, 1978
<i>Zalophus californianus</i>	3-4 mos.	11.7	12.0		960 (443)	4.0	Matsuura and Whittow, 1973
	2 yrs.	32	11.2		2449 (942)	3.7	Matsuura and Whittow, 1973
	2 yrs.	31.5	7.8		1675 (931)	2.6	Luecke, 1975
	3 yrs.	46.8	12.3		3937 (1253)	4.1	Pierce, 1970
	3-4 yrs.	54-69	6.2		2613 (1537)	2.0	Matsuura and Whittow, 1973
<i>Eumetopias jubatus</i>	Pup	13-21	7.8		926 (592)	2.6	Iversen and Krog, 1973
<i>Mirounga angustirostris</i>	Pup	106.9	4.9		3583 (2352)	1.6	Pierce, 1970
	Weaned	115-154	6.6		6044 (2540)	2.2	Ortiz, Costa, and LeBoeuf, 1978
	Weaned	83	4.4		3944 (1925)	1.4	Costa and Ortiz, 1980
<i>Odobenus rosmarus</i>	Young	54-66	7.2		3000 (1522)	2.4	Iversen and Krog, 1973

* Values in parentheses are predicted from weight (kg) according to the Kleiber (1975) equation $M = 70W^{3/4}$.

condition. The low resting rates measured by Øritsland and Ronald (1975) for adult harp seals were obtained from one animal believed to have liver damage and a second animal that was inactive yet permitted to dive freely, possibly experiencing a depression of metabolism associated with the dive (Scholander, 1940; Scholander *et al.*, 1942b) or a sleep condition (Miller, 1975; Miller *et al.*, 1976; Ohata, 1976), or both. Øritsland and Ronald (1975) suggested that their animals may have had a blubber content approaching 40% of total body weight. If so, the lean body mass had a high metabolism, since adipose tissue has low metabolic activity relative to lean tissue because of the "diluting effect" of a large triglyceride content (Wertheimer and Shapiro, 1948; Chernick, 1952; Miller and Blyth, 1953; Shapiro and Wertheimer, 1956; Davies, 1961; Muldowney, 1961; Bray and Atkinson, 1977). A combination of high body fat content and access to diving likewise may have produced the low resting metabolic rates observed by Parsons (1977) in five adult ringed seals and by Gallivan and Ronald (1979) in three adult harp seals.

Exercise Metabolism

Very few studies have been conducted on the energy cost of exercise in pinnipeds. Maximal metabolic effort has not been measured in any marine mammal. An apparent increase in oxygen consumption of swimming California sea lions (Pierce, 1970) as compared to the animals at rest (Matsuura and Whittow, 1973) led Costello and Whittow (1975) to examine the relationship between oxygen consumption and exercise level in trained

California sea lions. Estimating oxygen consumption from the measured oxygen debt, they found an initial increase in oxygen utilization while swimming, followed by a decrease to resting levels after 60 seconds of sustained activity. In contrast to the direct relationship between oxygen consumption and exercise level reported in terrestrial mammals (Taylor, Schmidt-Nielsen, and Raab, 1970), no correlation was observed between oxygen consumption and swimming speed in sea lions. On the other hand, Craig and Päsche (1980) did not measure a decrease in oxygen consumption with increased swimming duration of 2-year-old harbor seals. They obtained a positive correlation between oxygen consumption and swimming speed, based on measurements made during steady-state intermittent exercise.

Wekstein and Krog (1971) measured an increase in metabolism of 1.2 times the resting rate in a yearling harp seal permitted to swim freely in a tank. An increase in oxygen consumption of 1.8RMR was measured by Øritsland and Ronald (1975) in a swimming harp seal. Resting level, in this case, was estimated from the oxygen debt of a quietly diving seal, which may have been lower than in an actual non-diving condition of rest.

Diving Metabolism

Seals undergoing forced dives in the laboratory and prolonged dives in nature display a profound bradycardia or reduction in heart rate, essentially unaltered stroke volume, major redistribution of blood flow, and reduction of cardiac output (Elsner, 1969). These responses serve to

prolong the removal of oxygen from the blood and continue the perfusion of sensitive organs (brain and heart) at the expense of those more tolerant to asphyxia. A decrease in aerobic metabolism during long-duration dives was suggested by early observations that quietly diving seals did not repay their oxygen debt upon recovery (Scholander, 1940) and exhibited a lowering of temperature both at the body periphery and body core (Scholander *et al.*, 1942b). Lowering of peripheral temperature was attributed to the redistribution of blood circulation, and decreased core temperature was believed to result from an inhibition of aerobic metabolism by the accumulation of metabolites such as carbon dioxide and lactic acid (Scholander *et al.*, 1942a). Later observations revealed a decline in oxygen consumption (Kooyman *et al.*, 1973) and drop in body temperature of diving seals (Elsner, Hammel, and Heller, 1975; Kooyman, Wahrenbrock, Castellini, Davis, and Sinnott, 1980), supporting Scholander's (1942) suggestion of lower metabolic rate during the dive than at the surface. Hochachka and Storey (1975) demonstrated the high capacity of pinniped skeletal muscle for anaerobic glycolysis, enabling it to function despite removal from the blood circulation. Other studies revealed high glycogen levels in the brain of the Weddell seal, possibly enabling this normally aerobic tissue to tolerate the anoxic terminal stages of prolonged dives (Kerem, Hammond, and Elsner, 1973). Recent experimental evidence suggests that the heart, lung, and brain of diving seals have the ability to produce lactate or utilize it depending on the metabolic conditions (Murphy, Zapol, and Hochachka, 1980).

A comparison of metabolic rates observed during diving in several pinnipeds is presented in Table 13. The cardiovascular responses of seals during restrained diving are more intense than those measured during unrestrained diving (Elsner, 1965; Harrison and Ridgeway, 1975). Kooyman (1975) suggests that the profound cardiac slowing of forced dives in the laboratory in comparison to the lesser response of voluntary dives by wild seals reflects the range of dive pattern in nature from prolonged, exploratory or "emergency" dives with pronounced vasoconstriction and a large anaerobic component of metabolism to brief, shallow, aerobic dives. While investigating the diving characteristics of free-ranging Weddell seals, Kooyman, Castellini, Costa, Billups, and Piper (1979) determined that more than 97% of voluntary dives were aerobic: shorter than 26 minutes with little or no rise in blood lactate levels. In an earlier study, reduced oxygen consumption was observed during a long, deep dive by an adult Weddell seal, requiring full development of the dive response (Kooyman *et al.*, 1973). Scholander *et al.* (1942b) estimated the degree of metabolic decline in diving harbor seals to be as much as 50 to 60% of pre-dive levels, basing this estimate on body temperature measurements and knowledge of pre- and post-diving oxygen consumption.

Sleeping Metabolism

Sleeping mammals generally exhibit a greater degree of muscular relaxation and reduced tension than while awake, and characteristically have lower metabolic rates than those measured under basal conditions

TABLE 13. Metabolic rate associated with diving in pinnipeds.

Species	Age	Wt (kg)	Metabolic Rate (nRMR)	Source
Harbor seal (<i>Phoca vitulina</i>)	Young	20	0.5 - 0.6	Scholander, and Grinnell, 1942b (restrained)
	2 yrs.	42.5	1.6	Craig, and Päsche, 1980 (unrestrained)
Weddell seal (<i>Leptonychotes weddelli</i>)	Adult	425	0.8	Kooyman, Kerem, Campbell, and Wright, 1973 (unrestrained)
Harp seal (<i>Phoca groenlandica</i>)	Adult	105	1.0*	Øritsland and Ronald, 1975 (unrestrained)
	Adult	110- 170	1.0*	Gallivan, 1977 (unrestrained)

* Metabolic rate during diving considered equal to RMR.

(Benedict, 1938; Hoch, 1971; Swan, 1974). A 25% decline in heat production from basal levels has been measured in sleeping mice (Davis, 1937; Denckla, 1970), and values 80 to 88% of basal rates have been reported for human subjects (Benedict, 1938; Hoch, 1971). A state of sleep can be difficult to define in some mammals, such as horses and cattle, where a reclining position is not necessary for sleep and some degree of postural muscle tension is always present (Benedict, 1938). Respiration rate has been used in some cases to determine a sleeping condition, as in the elephant where the respiration rate may fall to 50% of resting levels when sleep is attained (Benedict, 1936).

The limited data on oxygen consumption of sleeping pinnipeds, whether hauled out or submerged (see Table 14), indicates a reduction of metabolic rate which, in phocine seals, appears similar in magnitude to that observed during quiet diving (Miller and Irving, 1975; Miller *et al.*, 1976). A depression of deep body temperature during sleep, observed in northern fur seals (Bartholomew, 1954), and young harbor seals (Miller and Irving, 1975), also suggests metabolic decline (Scholander *et al.*, 1942b). Sleeping seals frequently become apneic (Bartholomew, 1954; Kooyman *et al.*, 1973; Kooyman *et al.*, 1980). The similarity of cardiovascular and metabolic responses associated with apnea and diving have been noted by Irving (1939), Scholander (1962), and Lin, Matsuura, and Whittow (1972). The metabolic "economy" afforded by such responses may be of great adaptive value to a mammal with characteristically high resting metabolic rate (Irving, 1973).

TABLE 14. Metabolic rate associated with sleeping in pinnipeds.

Species	Age	Wt (kg)	Metabolic Rate	Source
Harbor seal (<i>Phoca vitulina richardsi</i>)	5 wks	10-13	0.65 RMR	Miller and Irving, 1975
	1-2 wks	13.5	0.75-0.85 BMR	Miller, Rosenmann, and Morrison, 1976
California sea lion (<i>Zalophus californianus</i>)	3-4 yrs	54-69	0.69 RMR	Matsuura and Whittow, 1973
Northern fur seal (<i>Callorhinus ursinus</i>)	Subadult	15-28	0.64-0.90 BMR	Ohata, 1976

Some pinnipeds appear to utilize sleep as a means of minimizing heat production during hyperthermia. Matsuura and Whittow (1973) noted a 24% decline in oxygen consumption from resting levels at a rectal temperature of 38.9°C in sleeping California sea lions exposed to air temperatures greater than 21°C. In the same study, an adult harbor seal appeared to sleep as air temperature rose from 21 to 35°C, maintaining a constant oxygen consumption as rectal temperature increased by 2°C. Miller and Irving (1975) observed a similar capacity for heat tolerance in young Bering Sea harbor seals, who slept frequently at air temperatures above upper critical (30°C) and underwent a 35% decline in metabolism. Oxygen consumption remained constant while rectal temperature increased more than 2°C under hyperthermic conditions. Oxygen consumption of sleeping 1 to 2-week-old harbor seals in water decreased to 15 and 25% of basal levels in the thermoneutral zone, and the tendency to sleep increased at higher water temperatures (Miller *et al.*, 1976). The seals were able to reach a steady state of oxygen consumption and body temperature at a water temperature of 37°C. Ohata (1976) suggested that the combined effects of reduced metabolism during sleep, increased peripheral vasodilation, and behavioral adjustments enabled his subadult northern fur seals to tolerate 26°C air for long periods.

Thermoregulation

Resting heat production is sufficient to maintain thermal homeostasis under most temperature conditions encountered by a terrestrial mammal in its natural environment (Scholander, Hock, Walters, and Irving,

1950). The same appears to be true for most pinnipeds that have been studied (Irving, 1973). Scholander (1940) observed no change in resting metabolism of a grey seal (*Halichoerus grypus*) immersed in 5°C water, typical of its natural habitat. Young Atlantic harbor seals (*Phoca vitulina concolor*), acclimatized to winter conditions, tolerated air temperatures from -10 to -25°C without elevation of resting metabolic rate (Irving and Hart, 1957). An increase in resting metabolism was noted for most of the seals in water colder than 10°C (the critical low), with one lean "runt" seal observed to have a critical low of 20°C in water and a higher resting rate in air and water at all temperatures tested. Seals with sufficient subcutaneous blubber were able to maintain basal heat production in cold water by cooling the peripheral tissues, thereby increasing their effective insulation and producing steep thermal gradients from body core to the external environment. In summer-acclimatized seals, Hart and Irving (1959) found the BMR to be the same in both air and water, with a difference in critical low of 2°C (winter) and 20°C (summer), and maintenance of a gradual thermal gradient through the blubber. They did not observe a lower critical temperature in two young harp seals tested in 0°C water. Gallivan (1977) was not able to detect an increase in resting metabolism of three adult harp seals tested in water from 1.8 to 28.2°C. Over a temperature range of 13 to 36.5°C in water, Parsons (1977) measured steady basal oxygen consumption for one adult ringed seal.

Matsuura and Whittow (1973) determined the upper critical air temperature for subadult California sea lions to be 21°C. Subadult northern

fur seals were able to maintain constant RMR at air temperatures from -7 to 33°C (Ohata, 1976). In 1 to 26°C water, the seals were generally active, although values of sleeping metabolism were obtained from 15 to 26°C which were in agreement with sleep values obtained in air. Shivering was observed in water with an oxygen consumption 8.8 times resting levels, and the frequency of high metabolic rates increased as water temperature decreased from 15°C. Miller (1978) observed that subadult northern fur seals were able to maintain basal levels of oxygen consumption in air from 0 to 20°C with lowest air temperatures still above lower critical. In contrast to Ohata's (1976) findings, BMR in water was attained only around 24°C, with metabolism increasing linearly with decreasing temperature below 20°C. The mean basal oxygen consumption of Miller's (1978) seals was about 17% higher than that of Ohata's (1976) seals (using minimal awake values) over the same air temperature range.

Newborn and nursing phocine seals, lacking the thick subcutaneous fat present in older animals, must employ other means to survive cold stress encountered after birth. Adaptive mechanisms which have been found to increase heat production in young terrestrial mammals include shivering and nonshivering thermogenesis, peripheral tissue vasoconstriction, postural adjustments, and accumulation of body fat (Bartholomew, 1977). Harbor seal pups (*Phoca vitulina richardsi*) shed their lanugo *in utero* and are born with a wettable, adult-like pelage. Like other newborn phocids, they lack well-developed subcutaneous fat and appear to be quite vulnerable to the thermal stress of cold water, rain, and wind exposure (Miller *et al.*, 1976). Miller and Irving (1975),

studying the oxygen consumption of 1 to 5-week-old harbor seal pups in air, noted a lower critical temperature of 3°C, with maintenance of body core temperature accomplished by peripheral vasoconstriction. Shivering was observed on a few occasions at air temperatures lower than -10°C, but was not considered to be an important means of increasing heat production. Older seals (3 to 5 months) had lower RMR's and a lower critical air temperature (-5°C). During tests in water with 1 to 2-week-old harbor seals, Miller *et al.* (1976) found identical BMR's in two seals, with a narrower thermoneutral zone apparent in a leaner pup. Exposure to 5°C water presented only a modest cold stress, requiring a two-fold increase in metabolism over basal.

Harp and Weddell seal pups are born with a lanugo which generally provides poor insulation when wet. Very young harp seals have not been observed to utilize shivering as a means of heat production (Grav, Blix, and Päsche, 1974). Recent discovery of extensive subcutaneous brown fat deposits in very young harp seal pups (Grav *et al.*, 1974) and demonstration of its thermogenic activity (Grav and Blix, 1976) suggest the major importance of nonshivering thermogenesis in body temperature maintenance of neonatal harp seals. These deposits become rapidly depleted with age (Grav *et al.*, 1974). Davydov and Makarova (1964) noted a steady decline in oxygen consumption with age of harp seal pups exposed to cold air and water, and attributed this change to an age-related increase in blubber thickness. Iversen and Krog (1973) reported a lower critical air temperature of 8°C in harp seal pups undergoing their first molt, a time when fat reserves may be depleted after a period of fasting. Elsner *et al.*

(1977) observed elevated RMR's in newborn and pre-nursing Weddell seals which decreased with age and blubber accumulation. Shivering was observed in newborn pups and in seals younger than 10 days, and no evidence of brown fat was found in histological examinations of fetal tissues.

In this study, the basal, thermoregulatory, active, and maximal metabolic capacities of captive harbor and spotted seals were obtained from measurements of oxygen consumption using open-circuit respirometry. These measurements formed the basis for estimating the maintenance energy requirements of different age groups of seals.

Methods and Materials

Metabolism Experiments

Oxygen consumption and carbon dioxide production were measured in 11 captive harbor seals (*Phoca vitulina richardsi*) and five spotted seals (*Phoca largha*) comprising five general age classes: 0.2 to 0.7 years (pup), 1 year (yearling), 3 years (juvenile), 4 years (subadult), and 9 years (adult). The dates, descriptions of seals tested, and air and water temperatures of each experimental set are summarized in Table 15. The animals were in a postabsorptive state (12 to 20 hours after feeding) and were allowed to dry completely before tests in air to minimize evaporative heat loss. All tests, except those involving the 9-year-old seals, were conducted at the Institute of Arctic Biology Animal Facility, University of Alaska, Fairbanks, in temperature-controlled rooms ($\pm 1^{\circ}\text{C}$) as previously described. During tests in air in the

TABLE 15. Metabolic tests in air and in water on five age classes of harbor (H) and spotted (S) seals.

Year	Season	Temperature (°C)		Age (yrs)	Sex	Number Tested	Mean Body Wt. (kg)	Species
		Air	Water					
1976	Fall	0	+4	0.5	♂+♀	2	23.0	S
1977	Spring	0	+4	1.0	♀	1	36.0	S
		0	+4	3.0	♂+♀	2	42.7	H
1977	Summer	+20	+10	0.2	♂+♀	6	17.8	H
		+20	+10	1.0	♀	1	38.6	S
		+20	+10	3.0	♂+♀	2	47.8	H
1977	Fall	0	+4	0.3	♂+♀	6	21.1	H
		0	+4	1.0	♀	1	38.6	S
		0	+4	3.0	♂+♀	2	47.8	H
1977	Winter	-20	-1.8	0.7	♂+♀	6	28.5	H
		-20	-1.8	1.0	♀	1	46.3	S
		-20	-1.8	3.0	♂+♀	2	49.8	H
1978	Spring	0	+4	4.0	♂+♀	2	50.8	H
		—	+16	9.0	♂+♀	2	72.3	S
1978	Fall	0	--	4.0	♂+♀	2	46.9	H

temperature-controlled room, each seal was placed in an aluminum chamber 0.9 x 0.5 x 0.5 m fitted with a clear plexiglass lid which permitted observation. Tests in water were conducted in the same room with each seal placed in a 1.2 x 0.6 x 0.6 m steel-framed polyethylene chamber provided with a plexiglass lid and filled to a depth of 0.4 m. The air space, before addition of the seal, was about 0.14 m³. Salt was added to the chamber water to achieve a water temperature of -1.8°C without freezing in winter. Tests of 9-year-old seals in air and water were conducted at the School of Hygiene and Public Health, The Johns Hopkins University, Baltimore, with each animal placed in a 2.0 x 0.8 x 0.8 m aluminum-framed plexiglass chamber set in a temperature-controlled room ($\pm 2^\circ\text{C}$). When used for tests in water, this chamber was filled to a depth of 0.6 m and had an air space of 0.32 m³ before the seal was added. Air flow rates of 30 to 80 l/min in the chambers were required for seals ranging in weight from 18 to 73 kg to maintain carbon dioxide levels below 1%. Air and water temperatures in the chambers were measured by copper-constantan thermocouples, with all readings displayed on a digital readout thermometer (Fluke Model 2100A). Rectal temperatures before and after the experiment were measured in half of the tests, using a calibrated thermocouple probe inserted 15 cm. Recordings were begun at least 1 hour after each seal was placed in the chamber to allow establishment of a thermal steady-state and, for tests in water, to permit equilibration of chamber air with dissolved carbon dioxide. The time required for 95% equilibration of the Fairbanks air chamber to a change in oxygen consumption, as predicted by the equation of Silver

(1946), was calculated to be 22 to 7 minutes over a range of flow from 30 to 90 l/min. For the Fairbanks water chamber, the time for 95% equilibration was calculated to be 14 to 5 minutes over the same range of flow. The Baltimore air chamber was 95% equilibrated to a change in oxygen consumption after 41 minutes at 90 l/min when used for experiments in air, and after 10 minutes at 90 l/min when used for experiments in water. The actual times required for the 95% response were much less than these estimates, possibly as a result of partial displacement of the air column by the seal itself. Calculations of oxygen consumption (in all tests) and carbon dioxide production (in half of the tests) were calculated for periods of stable respiratory exchange and constant behavior at least 15 minutes in duration according to the equation of Depocas and Hart (1957). During apneustic periods associated with sleep and diving, a planimeter was used to integrate the area beneath each record tracing to obtain a mean value of the volume fractional concentration of each gas in expired air.

A stopwatch was used to obtain dive duration (time between submer-
sion and emersion), as observed through the chamber lid. Mean values of oxygen consumption under basal conditions were considered significantly different if $P < 0.05$ according to Student's "t" distribution.

Exercise Experiments

Three captive harbor seals, two males and one female 0.3 to 1.3 years old, were trained to carry increasing workloads provided in a weighted canvas jacket while treading water in a cylindrical tank

connected to an open-flow system. The tank consisted of a 1.8 m high, 0.6 m diameter section of aluminum highway culvert, with a welded bottom and upper rim of 2-mm thick aluminum plate (Figure 13). The tank could be drained within 15 sec through a 10-cm diameter opening at the bottom. The lid was fitted with air inlet and outlet ports and small openings for thermocouples and harness line. A clear plexiglass lid with a latex rubber gasket was secured to the tank rim by adjustable steel clamps. Experiments were conducted in a temperature-controlled room ($\pm 2^{\circ}\text{C}$) with the tank filled to a depth of 1.6 m with 8°C fresh water. The tank was located adjacent to a 1.2-m high platform on which the open-flow apparatus was situated and from which the investigator had a clear view of the seal in the tank. The weighted jacket consisted of heavy-duty cotton-duck canvas with openings for the foreflippers and a row of pockets encircling the seal's thorax (Figure 14). The jacket was laced along the animal's back with thin latex-rubber tubing through brass grommets in the canvas. This lacing permitted thoracic expansion during exercise. The seal was held at the water surface by a rope attached to the jacket just above the pockets. With the seal in the tank, the rope was passed through a small opening in the plexiglass lid and was held by the investigator observing the seal. Lead diver's weights were added to the pockets before each experiment. Preliminary tests were run before each experiment to determine the weight load necessary to produce maximal steady-state exercise of at least 10 minutes duration. Seals were in a postabsorptive state for the tests and were thoroughly acclimated to test conditions before actual measurements were begun. Measurements

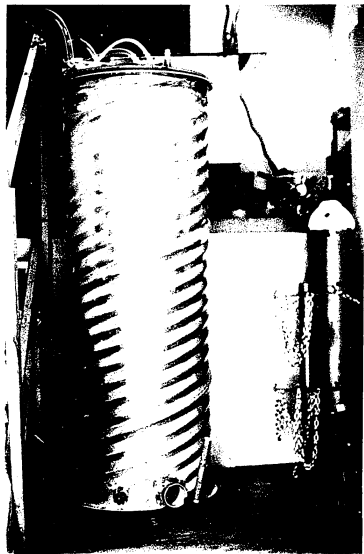


FIGURE 13. Cylindrical exercise tank used in combination with open-flow respirometry for measurement of maximal oxygen consumption in seals.



FIGURE 14. Young harbor seal wearing weighted jacket preparatory to treading exercise in cylindrical tank.

were begun at least 1 hour after the seal was placed in the tank, after a thermal steady-state had been attained and tank air had equilibrated with dissolved carbon dioxide. The time required for 95% equilibration of chamber air to a change in oxygen consumption was computed to be 7 minutes at a flowrate of 90 l/min, according to Silver's (1946) equation. A steady-state of oxygen consumption was actually attained within 5 minutes, evident as steady-state fractional oxygen concentration on the recorded output of the analyzer. In each experiment, after measurement of at least 10 minutes of rest at the water surface, the line was slackened and the seal permitted to tread water. Seals generally reacted quickly to the release of the line and weight of the jacket; they initially sank to the bottom, then swam vigorously to the water surface and maintained their position there, treading water with strong lateral movements of the hindflippers and pelvis. Seals which attempted to dive to avoid the treading exercise were returned to the water surface by a tug of the line. Tiring animals were returned to the surface and tied in place. Oxygen consumption (in all tests) and carbon dioxide production (in half of the tests) were calculated as previously described (Depocas and Hart, 1957) for sections of the record exhibiting maximal steady-state respiratory exchange for a minimum of 10 minutes. Pre- and post-exercise rectal temperatures were measured in half of the tests using a calibrated thermocouple probe inserted 15 cm. Tank air and water temperatures were continuously monitored with copper-constantan thermocouples, with readings displayed on a digital readout thermometer (Fluke Model 2100A).

Since the number of seals tested was small, each value of maximal oxygen consumption ($\dot{V}_{O_{2max}}$) obtained during a 10-minute period of steady-state exercise was considered to be a separate statistical event. Means were considered to be significantly different if $P < 0.05$ according to Student's "t" test.

Results and Discussion

Resting Metabolism in Air and in Water

Oxygen consumption values for pup, yearling, and juvenile seals (0.2 to 3.0 years old) at rest in air and in water at seasonal temperatures comparable to those encountered in the natural environment of the Bering Sea (Zenkevich, 1963) ranged from 8.0 to 8.7 ml O_2 /kg·min (2.6 to 2.9 watts/kg) in more than 50 replicate experiments. In each age group having male and female representatives (pup harbor and spotted seals and juvenile harbor seals), differences in RMR between sexes in air and in water were not significant within seasons or within species. Differences between the pooled means of each age group (males and females, in air and in water) in each season also were not significant. RMR's were not significantly different between harbor and spotted seals in each age group within seasons. Mean RMR's for harbor and spotted seal pups, a yearling spotted seal, and juvenile harbor seals over all seasons in air were 8.6 ± 0.1 , 8.3 ± 0.2 , and 8.4 ± 0.1 ml O_2 /kg·min, respectively. In water the means were 8.5 ± 0.1 , 8.2 ± 0.2 , and 8.4 ± 0.1 ml O_2 /kg·min, respectively. Since these values were the same at all air

and water temperatures tested and were in agreement with BMR's obtained for young harbor seals in air and in water by Miller and Irving (1975) and Miller *et al.* (1976), the environmental temperatures used were assumed to be within the thermoneutral zone of the seals. In addition, because these oxygen consumption values were obtained from resting, postabsorptive animals apparently at thermoneutrality, they were considered to be basal rates. Changes in rectal temperature, during representative, long-duration tests at each air and water temperature for individual seals, are shown in Table 16. These seals were quiet throughout the experiments and changes in rectal temperatures were small with no corresponding changes in metabolic rate. The mean respiratory quotient for all BMR measurements was 0.75 ± 0.4 , indicative of a lipid-based metabolism, and similar to results obtained on BMR studies of other phocine seals (Parsons, 1977).

The oxygen consumption of one 4-year-old (subadult) female harbor seal, tested at -20°C in air during winter 1977 and at 0°C in air in six separate experiments during spring and fall 1978, decreased from a mean value of 8.5 ± 0.2 ml $\text{O}_2/\text{kg}\cdot\text{min}$ obtained during winter 1977 to a mean of 7.2 ± 0.2 ml $\text{O}_2/\text{kg}\cdot\text{min}$ obtained during spring and fall 1978. This animal was considered to be approaching sexual maturity on the basis of Bishop's data (1967) on Gulf of Alaska harbor seals and Burns and Gol'tsev's (in preparation) data for harbor seals of the Aleutian Ridge and Pribilof Islands. A 4-year-old male harbor seal tested during the same time period maintained a BMR of 8.5 ± 0.1 ml $\text{O}_2/\text{kg}\cdot\text{min}$ that was significantly different from that of the 4-year-old female ($P < 0.05$).

TABLE 16. Rectal temperatures of harbor (H) and spotted (S) seals before and after metabolic tests in air and in water.

Species	Age (yrs)	Temp. (°C)		Duration of Test (hrs)	Initial T_{Re} (°C)	Final T_{Re} (°C)
		Air	Water			
H	0.3	0		3	37.1	36.6
S	1	0		3	37.2	36.9
H	3	0		4	37.4	37.0
H	0.7	-20		4	37.4	36.9
H	3	-20		4	37.4	36.9
S	1	+20		4	37.1	37.6
H	3	+20		3	36.9	37.7
H	3		+4	2.5	37.6	37.3
H	0.3		+4	3	37.1	36.6
H	0.7		-1.8	4.5	37.0	36.5
H	0.2		+10	3	37.4	37.3

This animal was not yet sexually mature. The BMR for the one 9-year-old (adult) male spotted seal during a test in air at +16°C was the lowest recorded. Over a 2-hour period, oxygen consumption of this seal remained steady at 5.4 ± 0.1 ml O₂/kg·min.

A plot of mean basal oxygen consumption against age is presented in Figure 15, which includes the data of Miller and Irving (1975) and Miller *et al.* (1976) for harbor seals younger than 5 weeks, and data from an Atlantic harbor seal, *Phoca vitulina concolor* (Ashwell-Erickson, unpublished). Basal metabolism decreased rapidly from birth to weaning, possibly a consequence of improved insulation resulting from deposition of subcutaneous fat following birth (Davydov and Makarova, 1964; Elsnér *et al.*, 1977). Oxygen consumption remained relatively stable until age 4, at which time it declined in the female seal tested but remained stable in the male. This difference may be attributable to the female's having attained sexual maturity; the approximate age range for sexual maturity in the male is about two years later (Bishop, 1967; Pitcher and Calkins, in press). Beyond the age of sexual maturity, BMR apparently continues to decrease until attainment of physical maturity, which is about 6 to 9 years in both harbor and spotted seals (Tikhomirov, 1971; Naito and Nishiwaki, 1972; Pitcher and Calkins, in press). A similar decline in metabolic rate has been observed from puberty to old age in humans (Kleiber, 1975) and other mammals (Denckla, 1970). The general trend of the metabolic decline with increasing age of seals correlates with the observed decrease in food consumption (Figure 5) and increase in body weight (Figure 6). When compared with mammalian standard

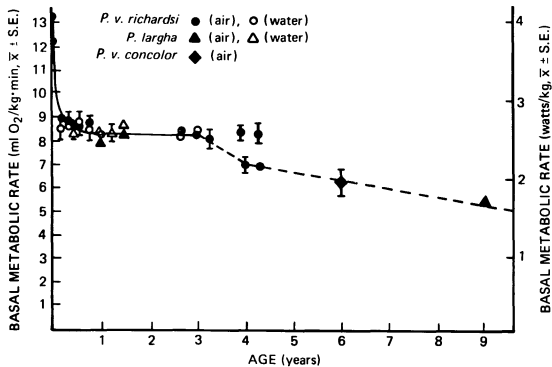


FIGURE 15. Variation of mean basal metabolic rate with age for Bering Sea harbor and spotted seals, with data for an Atlantic harbor seal (*Phoca vitulina concolor*) added for comparison. Curve fitted by eye.

metabolic rates (SMR's) as predicted by the Kleiber (1975) equation in Figure 16, the rates obtained for these seals were 2.4 to 1.5 times greater, those of the physically mature seals approaching the predicted mammalian values when computed on the basis of total body weight.

Metabolism During Sleep and Normal Activity

Measurements of oxygen consumption during sleep and various states of normal physical activity in captive harbor and spotted seals, together with those from other pertinent studies, are presented in Table 17. Three levels of sleep were identified which were metabolically the same both in air and in water: *Level 1*, light sleep or "doze" lasting from 1 to 15 minutes from which animals were easily awakened and during which metabolism ranged from 85 to 90% of BMR; *Level 2*, sleep lasting from 10 to 60 minutes with metabolism at 70 to 81% of BMR; *Level 3*, heavy or deep sleep lasting several hours with metabolism at 60 to 69% of BMR. Sleep was characterized by long apneustic periods which produced wave-like record tracings extending nearly full-scale in some instances (Figure 17). Although respiratory frequency was not monitored for seals sleeping in air, a qualitative measure of the length of apneusis was possible from the degree of respiratory excursion (distance between high and low values of oxygen consumption) represented by the tracing. In all animals tested, the apneusis increased as the level of sleep increased from *Level 1* to *Level 3*. Sleep in water was characterized by dives of varying duration: *Level 1*, dives of 1 minute and less; *Level 2*, dives of 1 to 3 minutes; *Level 3*, 3 to 5 minute dives. While

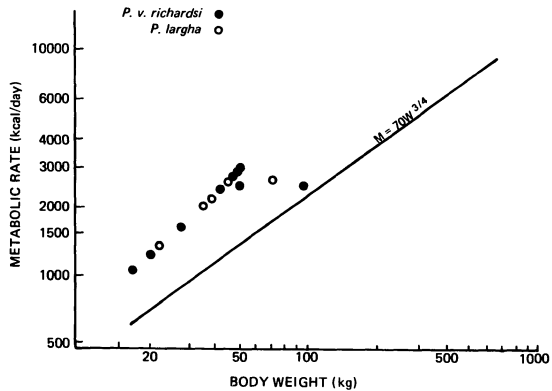


FIGURE 16. Mean basal metabolic rate (kcal/day) of harbor and spotted seals in relation to body weight and to the Kleiber equation $M = 70W^{3/4}$.

TABLE 17. Sleeping and activity metabolism expressed as multiples of the basal metabolic rate (BMR) in several age groups of harbor and spotted seals.

Age	Metabolism in Air					Metabolism in Water							
	Sleep			Active		Sleep			Active				
	1	2	3	1	2	1	2	3	1	2	3	4	5
1-2 wks	--	--	--	--	--	0.85	0.75	--	--	--	--	--	--
2-8 mos	0.87	0.70	0.66	1.2	1.7	0.87	0.76	0.69	1.1	2.1	2.2	1.1	1.3
1 yr	0.87	0.81	--	1.3	1.7	0.88	--	0.67	--	2.0	2.2	0.91	1.1
3 yrs	0.87	0.75	--	1.3	1.8	0.88	0.76	0.65	1.3	1.7	1.9	0.96	1.1
4 yrs, ♂	0.90	0.70	0.60	1.3	1.6	--	--	--	--	1.8	--	--	--
4 yrs, ♀	0.89	--	0.67	1.3	1.6	--	--	--	1.6	1.8	--	--	--
9 yrs	--	--	--	--	--	0.89	0.72	--	--	--	--	--	--

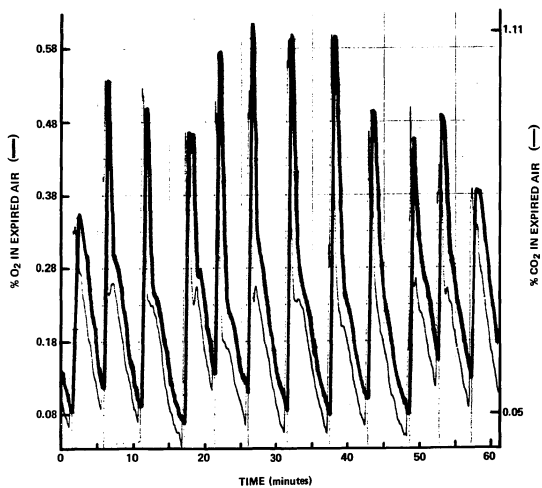


FIGURE 17. Record tracing of oxygen consumption (heavy line) and carbon dioxide production (light line) of a seal sleeping in water, measured by open-flow respirometry.

sleeping in water, the seal remained submerged in one area of the tank, eyes closed, rising rhythmically to ventilate, then submerge again. The mean RQ for all sleeping episodes in air in which carbon dioxide production was measured was 0.72 ± 0.05 ($n = 22$); for those in water the RQ was 0.68 ± 0.04 ($n = 24$).

Five levels of activity were defined in terms of characteristic behavior with relatively stable levels of metabolism: *Level 1*, alert (looking, moving head); *Level 2*, agonistic behavior (pawing, lunging, biting); *Level 3*, vigorous surface swimming; *Level 4*, quiet diving of 3 to 5 minutes duration; *Level 5*, "exploratory" diving, consisting of 3-minute or less dives with underwater swimming. The highest energy costs were incurred during agonistic behavior in air (*Activity Level 2*) and vigorous surface swimming in water (*Activity Level 3*) for all age classes studied. These costs were low in comparison to those of other large mammals performing similar activities (Schmidt-Nielsen, 1972). Quiet diving (*Level 4*) was characterized by a reduction of metabolism from 91 to 96% of BMR in seals 1 year and older, and was about the same as BMR in seals 0.2 to 0.7 years old. The energy cost of exploratory diving (*Level 5*) in all seals was greater than that of quiet diving, probably as a result of swimming during the dive. Increased metabolism during dives presumably as a result of swimming has been observed in penguins (Scholander, 1940), manatees (Scholander and Irving, 1941), and muskrats (Fairbanks and Kilgore, 1978). The mean RQ's measured for all activity levels were not significantly different, and the mean for all activities was 0.69 ± 0.01 , suggestive of a lipid-based metabolism.

Metabolism During Maximal Muscular Exercise

The results of 14 exercise experiments on three young harbor seals are shown in Figure 18. One female seal was tested at various times from ages 0.2 to 1.0 year, and two males were tested at 1.3 years of age. Maximal oxygen consumption ($\dot{V}_{O_{2max}}$) was attained after 5 to 10 minutes of steady-state muscular exercise and resulted in no significant differences among the three animals tested (32.8 ± 2.8 ml O_2 /kg·min or 10.8 ± 0.9 watts/kg) at different workloads in water (2.4, 6.4, and 8.0 kg). Successively higher workloads were necessary to attain the same $\dot{V}_{O_{2max}}$ in the female seal from 0.3 to 1.0 year of age. Workloads higher than 8.0 kg applied to all three seals at 1.3 years produced the same $\dot{V}_{O_{2max}}$ but caused exhaustion within 5 minutes. Measurements of rectal temperature in two seals immediately before and after maximal exercise in separate experiments revealed a rise in body temperature of 2°C. In three tests, RQ's averaged 0.72 ± 0.03 during rest, and 0.83 ± 0.03 during maximum steady-state exercise. The increase in RQ indicated lactate buildup as a result of anaerobic metabolism in the muscles. The metabolic scope, or range of metabolic increase from basal to maximal levels (aerobic capacity), was equivalent to 4BMR, which is considerably lower than corresponding values measured for other large mammals but similar to those obtained for some rodents and the sea otter (Table 18). The reduced metabolic scope for activity in harbor seals, sea otters, and small rodents may be related to the high mass specific oxygen

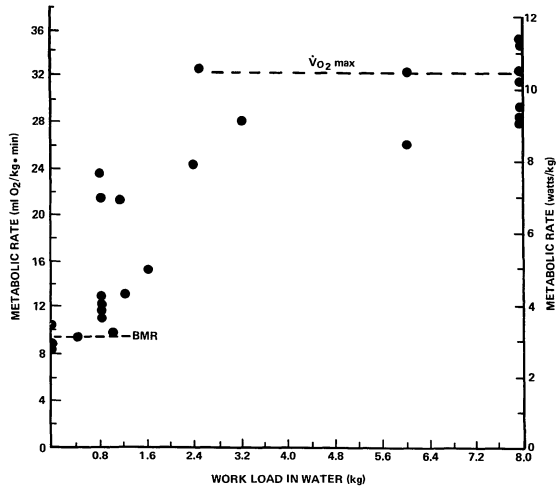


FIGURE 18. Oxygen consumption *versus* work load in water for three thermo-neutral young harbor seals treading water in an exercise tank.

TABLE 18. Relation of standard to maximal oxygen consumption in several mammals.

Species	Body Mass (g)	$\dot{V}_{O_2} \text{ max} / \dot{V}_{O_2} \text{ std}$	Source
Harbor seal (<i>Phoca vitulina richardsi</i>)	250000	4.0	This study
Sea otter (<i>Enhydra lutris</i>)	33000	4.0	Morrison, Rosenmann, and Estes, 1974
	38000	3.2	Costa, in press
Common mouse (<i>Mus musculus</i>)	33	7.2	Pasquis, Lacaille, and Dejours, 1970
Hamster (<i>Cricetus auratus</i>)	100	6.5	Pasquis <i>et al.</i> , 1970
Rat (<i>Rattus norvegicus</i>)	376	6.9	Pasquis <i>et al.</i> , 1970
Guinea pig (<i>Cavia cobaya</i>)	840	6.3	Pasquis <i>et al.</i> , 1970
Dog (<i>Canis familiaris</i>)	6300	11.1	Chatonnet and Minaire, 1966
	10000	23.7	Young, Mosher, Erve, and Spector, 1959
	24000	21.7	Cerretelli, Piiper, Mangili, and Ricci, 1964
Man (<i>Homo sapiens</i>)	65400	16.7	Åstrand, 1952
	70000	21.4	Brody, 1945
Horse (<i>Equus equus</i>)	282000 (pony)	20.6	Brody, 1945
	677000 (draft)	21.0	Brody, 1945

consumption of these mammals at rest or to natural selection for ability to incur a large oxygen debt during short bursts of intense activity (Irving, 1973; Bartholomew, 1977). The similarity of basal, sleeping, and active energy costs in harbor and spotted seals suggests comparably narrow aerobic capacities in both species.

Summary

Captive Bering Sea harbor and spotted seals 0.2 to 9.0 years old exhibited BMR's 2.4 to 1.5 times greater than those predicted for terrestrial mammals of similar size from Kleiber's (1975) equation. Basal heat production apparently was sufficient to maintain thermal homeostasis in air and water temperatures typical of their natural environments. Basal metabolism in harbor and spotted seals declined rapidly from birth to weaning as subcutaneous fat was acquired, and remained stable until breeding age. A further, more gradual decline took place to the age of physical maturity. Older, physically mature seals may exhibit basal metabolic rates similar to those of terrestrial mammals of comparable weight, possibly as a result of fat accumulation.

Sleeping and diving were energy-conserving activities, comprising only 60% (sleeping) to 96% (diving) of basal energy expenditure. The energy cost of swimming, alert, and agonistic behaviors were lower than similar activities in other mammals. The metabolic scope of these seals was about 4BMR, which also is low in comparison with the aerobic capacities of other large terrestrial mammals, but similar to those of sea otters and small rodents. Energy costs of activity in harbor and spotted

seals are well within the bounds of maximal aerobic capacity. This suggests that evolutionary selection in these mammals has favored the ability to incur a large oxygen debt rather than a large metabolic scope.

CHAPTER VI

ENERGY UTILIZATION: ESTIMATION OF NET ENERGY FOR PRODUCTION



Introduction

Production energy (NE_p) is that component of the net food energy which is used in the formation of new body tissues (lean tissue in body growth and hair replacement during molt), energy reserves (body fat), and in reproduction (formation of gametes, young, and milk). Postnatal body growth, body fat production, and the molting process have been examined to some extent in pinnipeds, while the energy requirements of reproduction have only been hypothesized (Lavigne *et al.*, 1977).

Postnatal Growth

The postnatal growth curves of pinnipeds are comparable to those of most terrestrial mammals in that they comprise a steep, initial increase in body size or "self-accelerating" growth phase followed by a gradual or "self-inhibiting" growth phase (Brody, 1945; Laws, 1959). The early, "self-accelerating" phase reflects a tendency of indefinite multiplication (one body cell giving rise to two, two cells to four, etc.). Once an individual reaches a certain body size, environmental limitations restricting unlimited expansion (e.g., the ability of the body to supply its cells with nourishment and remove wastes) retard the intrinsic growth rate and the slope of the curve changes from accelerating to decelerating. The point of inflection generally coincides with sexual maturity in mammals (Brody, 1945). Growth finally ceases at physical maturity, although maintenance continues.

Much accurate information is available on the growth rates of wild pinnipeds, partly as a result of the discovery and implementation of

ageing techniques based on tooth examination (Scheffer, 1950; Laws, 1952, 1959), and the initiation of large-scale mark-recapture experiments on commercially important pinnipeds (Laws, 1959). In the construction of pinniped growth curves, body length has often been used as an index of size in preference to body weight, which is more susceptible to seasonal fluctuations. Standardized methods have been developed for pinniped body measurements (American Society of Mammalogists, 1967) which have contributed greatly to the uniformity and reproducibility of morphometric data among species.

Laws (1959) compared data on the growth patterns of 11 phocids, two otariids, and one odobenid, noting that smaller species grow at a slower rate than larger ones and that longevity is directly correlated with rapid growth rate. Laws also showed that the average length at sexual maturity in females (age of first ovulation) of 12 pinniped species was 86.6% of the final body length, suggesting that near-completion of growth before parturition minimized competition between a still-growing female and her rapidly-growing offspring. Bryden (1968) examined the different developmental sequence of pinnipeds in comparison to terrestrial mammals. Initial postnatal growth results principally from blubber deposition during nursing, followed by increase in organ size, muscle mass, and body length. The typical pattern in terrestrial mammals is from nerve tissue to bone, muscle, and fat (Bryden, 1969; Lavigne *et al.*, 1977). Subsequent studies have provided additional information on the growth characteristics of phocids such as the elephant seal, harp seal, spotted seal,

harbor seal, and otariids such as the northern fur seal and Antarctic fur seal.

The growth pattern of the southern elephant seal, *Mirounga leonina*, is the best known of any phocid (Ling, 1966). A difference in growth and age of sexual maturity between the populations of this species at Macquarie and Heard Islands and the population at South Georgia was attributed to pressures retarding postnatal development and breeding (Bryden, 1968). Bryden (1968) identified overcrowding within the seal harems as the major factor responsible for growth stunting and delayed sexual maturity. This disturbance was alleviated in the South Georgia population as a result of long-term sealing operations which altered the herd structure.

Sivertsen (1941) studied the growth and development of harp seals (*Phoca groenlandica*) in relation to commercial productivity, but without accurate ageing techniques. Age determinations from tooth sections in harp seals have since yielded estimates of 6 years as the mean age of sexual maturity (age at first ovulation) in females from undisturbed populations, and 4 years in heavily-exploited populations (Sergeant, 1966). Males are believed to mature at 8 years of age (Bryden, 1974).

Bishop examined postnatal growth in Pacific harbor seals (*Phoca vitulina richardsi*) collected at Tugidak Island in the northern Gulf of Alaska. From birth to weaning, males and females increased weight rapidly to about 72% over birth weight. At 5.5 months of age, males were consistently heavier than females and continued to increase in body length until 10 years. The growth of females (length and weight)

declined markedly after age 5. Females were considered sexually mature at 3 to 4 years of age. Bishop's data suggested that males and females attained 75% of their full-grown weight by sexual maturity, at which time females also attained 84% of their full-grown length.

Bigg (1969) made a comprehensive study of Pacific harbor seals in British Columbia, from which Bryden (1974) was able to derive mean length/age curves for males and females. Males and females grew at the same rate from birth to 5 years, at which time the females were physically mature (full-grown) and beyond which males continued to grow until physical maturity at 9 years. Most males were sexually mature at 5 years and females at 3 years (at first ovulation).

Growth curves (weight/age and length/age) were constructed for Pacific harbor seals at the Prince William Sound-Copper River Delta area (Pitcher, 1977) and Kodiak region (Pitcher and Calkins, in press), with geographic comparisons of adult body size in harbor seals throughout the Gulf of Alaska (Pitcher and Calkins, in press). In the Prince William Sound-Copper River Delta area, maximum skeletal size (physical maturity) was attained at 7 years in both males and females, although weight continued to increase. Males were generally heavier and longer than females at all ages. Linear growth for both sexes of Kodiak harbor seals was rapid from birth to 4 or 5 years of age, after which it slowed until physical maturity was attained at age 7. Weight increased rapidly from birth to age 5 and then slowed until a maximum was reached at 10 years. Adult males were generally longer and heavier than adult females. The mean age of first ovulation in female harbor seals was 5

years, and the age of productive maturity (age of first successful pregnancy) was estimated as 5.5 years. The oldest male collected was 26 years of age and the oldest female was 31 years. Birth lengths and weights were greater for Kodiak harbor seals than for those from the Icy Bay and Yakutat Bay areas. Seals from Kodiak, Kenai, Prince William Sound, and the Alaska Peninsula were larger (longer and heavier) than those from Lower Cook Inlet and Icy Bay and Yakutat Bays. Burns and Gol'tsev (in preparation) have noted a similar increase in body size of Pacific harbor seals progressing westward from the Aleutians to the Pribilof and Commander Islands.

Postnatal growth in spotted seals has been studied in populations of the Bering Sea (Tikhomirov, 1971) and waters surrounding Hokkaido (Naito and Nishiwaki, 1972). Tikhomirov (1971) constructed length/age curves for 122 male and 109 female spotted seals from the Bering Sea, noting that females lagged behind males in growth after the first year. The age of sexual maturity in the female was 4 years and about 5 years in the male. Physical maturity was attained at 8 years in the female and 9 years in the male. At the time of first ovulation, females were approximately 4 years old and weighed 68.3 kg on the average, with nearly 92% of their final body length attained. Males were about 5 years old at sexual maturity, had a mean weight of 78.4 kg, and also were about 92% of their final body length. Postnatal growth curves were constructed from length/age data collected from 150 male and 176 female spotted seals in the Hokkaido area by Naito and Nishiwaki (1972). First year growth rates for both sexes were the same as those observed

for the Pacific harbor seal by Bigg (1969) and lower than those reported by Tikhomirov (1971) for Bering Sea specimens. Both sexes grew at similar rates until 5 years of age, beyond which females continued growth until 10 to 11 years and males until 14 to 15 years, the approximate age ranges for physical maturity. The length of physically mature females averaged 94% of that in physically mature males. The oldest seals collected were a 26-year-old male and a 32-year-old female, in comparison to the 29-year-old male and 35-year-old female reported by Tikhomirov (1971).

Growth patterns in the northern fur seal, *Callorhinus ursinus*, are perhaps among the best documented in pinnipeds because of the extensive investigations conducted during commercial harvesting on the Pribilof Islands (Bryden, 1974). Scheffer and Wilke (1953) reported postnatal growth patterns in *Callorhinus*, noting that females become sexually mature by age 5 (first ovulation) and males at 5 to 6. A detailed comparison of growth characteristics in northern fur seals and Antarctic fur seals (*Arctocephalus gazella*) was made recently by Payne (1979). *Callorhinus* and *Arctocephalus* exhibit similar growth rates during the suckling period, with growth in *Arctocephalus* becoming more rapid from the post-weaning phase to age 5. At age 5, *Callorhinus* males grow at a faster rate, becoming larger than *Arctocephalus* males. The shape of the growth curves in females of both species is identical, with a near-constant difference in length of about 8 cm maintained between the two until about 12 years of age. Payne (1979) attributes these variations in early growth pattern to the difference in stability of the two fur

seal stocks, *Callorhinus* having been maintained at nearly constant population levels for 40 years, and *Arotocephalus* recovering from recent over-exploitation.

Body Fat

Seasonal changes in the body fatness of pinnipeds are well-documented, and have been determined by field observations of blubber thickness in carcasses (Imler and Sarber, 1947; Fisher, 1952; McLaren, 1958; Hart and Fisher, 1964; Bishop, 1967; Elsner *et al.*, 1977; Pitcher, 1977; Pitcher and Calkins, in press), application of seasonal condition indices based on girth and length measurements (Sergeant, 1973) and the ratio of blubber weight to total body weight (Pitcher, 1977), estimates of body fat in live animals from skinfold thickness and radioisotope dilution experiments (Ohata, 1976; Kodama, Elsner, and Pace, 1977), and ultrasonic measurements of anesthetized animals combined with body volume calculations (Parsons, 1977). Chemical analyses of body composition in one species of phocine seal have yielded quantitative measures of body fat content in newborn and older animals (Stirling and McEwan, 1975).

Fisher (1952) measured the blubber thickness of newborn Pacific harbor seals from the Skeena River, British Columbia, and compared it to that of older pups collected after the birth season. He noticed a rapid increase in blubber accumulation from birth during May and June to a maximum at weaning in July, with a decrease thereafter until nutritional independence was attained. Bishop (1967) noted an increase in blubber thickness from birth to weaning in harbor seals collected at

Tugidak Island, Alaska. Elsner *et al.* (1977) measured mid-belly blubber thickness in Weddell seal pups, observing a rapid increase from 1 to 2 mm at birth to 1 cm at one week of age.

Imler and Sarber (1947) noted that harbor seals in southeastern Alaska were fattest in late winter and early spring when the blubber reached a thickness of 2.5 to 4.0 cm. Pregnant female harbor seals from Tugidak Island, Alaska, had greater blubber thickness than lactating females, and females which had completed lactation had the thinnest blubber layers (Bishop, 1967). Pitcher (1977) observed seasonal condition patterns in harbor seals of the Prince William Sound-Copper River Delta region, Alaska. Using blubber thickness and the ratio of blubber weight to body weight as indices of body condition, he showed a gradual increase in condition from fall to mid-summer, after which it declined rapidly in response to the demands of lactation, breeding, and molting. He suggested a sequence of fat depletion among age classes of seals, beginning with the rapid decline of lactating females, followed by breeding males, and finally the immature seals of both sexes during the molt. The seasonal pattern of blubber thickness in adult harbor seals of the northern Gulf of Alaska was determined by Pitcher and Calkins (in press), who reported high, stable levels of body fat from November to mid-May, followed by a decrease during the summer months. Lowest levels were recorded for the period from mid-July to mid-September, when many seals were molting. Female seals were consistently fatter than adult males, and their summer decrease in blubber thickness was attributed to the combined effects of lactation, breeding, and molting.

McLaren (1958) observed a decrease of body fat in ringed seals from late spring to early summer, and an increase from mid-summer to late fall. Parturient females lost fat rapidly from early April to early June as a consequence of lactation. Lønø (1970) reported a decrease in percent body fat of 75 adult ringed seals during mid-April and May from a winter high of 56% to a summer low of 35%. Body fat increased rapidly from late August to mid-September. Stirling and McEwan (1975) determined the body composition and caloric value of 12 ringed seal carcasses representing an age range from newborn to adult. They noted a marked increase in body fat from 13% in newborn seals to 45% in weaned pups, with 27% fat detected in three yearlings and 34% in one adult. The gross energy content of seals increased with age and blubber accumulation. Parsons (1977) measured blubber thickness at 10 points on the bodies of anesthetized ringed seals, utilizing an ultrasonic device calibrated against absolute measurements made on dead animals. These measurements were used to calculate the difference between total volume and blubber-free volume, and yielded estimates of body fat ranging from 23 to 60% for four adult seals.

Sergeant (1973) used a condition factor incorporating girth and length data to estimate the fat content of northwest Atlantic harp seals throughout the year. He noted a rapid decrease in body fat of adult females during lactation, and in males and immature seals during the molt, followed by a slow increase through the summer. Sivertsen (1941) reported a 31% reduction in blubber weight of female harp seals during

lactation in early spring. He estimated the average annual blubber content of adult harp seals to be about 40%.

Ohata (1976) estimated body fat in captive northern fur seals and Pacific harbor seals by measuring skinfold thickness at several body locations and by calculating the difference between total body weight and lean body mass as determined by radioisotope (tritium) dilution. Body fat in fur seals as estimated by skinfold thickness was maximal in winter and minimal in summer, with transition periods in spring and fall. Harbor seals had greater skinfold thickness at all body locations than fur seals. Body fat content in fur seals, as calculated from tritiated water experiments, was 15.6% during late winter and 5% in the fall, while harbor seals had 38% of body weight as blubber in late winter. Kodama *et al.* (1977) also used a tritium dilution technique to estimate seasonal fat changes in captive spotted seals maintained in California. The fat content of these animals increased to a maximum in winter and declined to a minimum in summer.

Molt

Studies of seasonal pelage cycles in mammals have been confined principally to hormonal and histological examinations of domesticated terrestrial species such as sheep, cattle, mice, rats, guinea pigs, and chinchillas (Lyne and Short, 1965), all of which exhibit discontinuous hair loss of short periodicity (Ling, 1972). Mammalian species which undergo annual pelage cycles involving generalized loss of body hair, termed "true molts" (Ling, 1972), have been examined to a lesser extent

and include terrestrial forms such as mink, weasels, ferrets, raccoons, and varying hares, and fur-bearing marine mammals such as sea otters, fur seals, and some phocine seals. The energy cost of molting itself, and in relation to the annual energy budget, has not been estimated for any mammal.

Factors involved in the control of pelage growth include the direct influences of thyroid, adrenal, and gonadal hormones, and the indirect effects of photoperiod and dietary and reproductive status (Ebling and Hale, 1970; Ling, 1970). Thyroxine has been shown to stimulate and the corticosteroids and adrenaline to inhibit hair growth in mammals exhibiting discontinuous pelage loss (Chang, 1926; Mohn, 1958; Bullough, 1962; Ebling and Johnson, 1964; Bullough and Rytömaa, 1965). Reports of thyroxine and corticosteroid effects in mammals undergoing true molts are conflicting (Reinke, Travis, and Dolnick, 1962; Rust, 1965; Rust, Shackelford, and Meyer, 1965), possibly as a result of inexact criteria for hormonal activity and indeterminate receptivity of the species to hormonal stimulation at specific times during the pelage cycle (Riviere, Engelhardt, and Solomon, 1977). Nutritional status may affect pelage growth through thyroid feedback or by producing stress which influences adrenal output or both (Ling, 1970). The role of gonadal hormones in hair growth regulation is unclear and may depend on a synergistic effect with other endocrine products (Ling, 1972). The interacting endocrine glands are coordinated with respect to seasonal photoperiod through the hypothalamic-hypophyseal system (Ebling and Hale, 1970; Ling, 1972).

Macroscopic study of molting in commercially valuable pinnipeds such as fur seals and young harp seals has been directed toward assessment of seasonal pelt quality and replacement of the birth coat (Scheffer, 1962). In a classic study, Bergersen (1931) made a detailed morphological description of the skin and hair of the harp seal and noted epidermal changes during the molt. The histology and histochemistry of harbor seal skin and hair were examined in detail by Montagna and Harrison (1957). Sokolov (1960) has noted the structure of skin and pelage in several pinnipeds in regard to thermoregulation. Scheffer (1962) made an exhaustive study of pelage and molting in the northern fur seal. The nature of the integument and hair growth process in the southern elephant seal was given in-depth treatment by Ling (1965, 1968, 1969). Few endocrine studies have been performed on pinnipeds during the molting cycle until recently (Riviere *et al.*, 1977; Engelhardt, 1977, 1979) and histological examination of epidermal changes during annual cycles in this group likewise have been limited.

With the development of improved facilities for the handling and care of captive pinnipeds, many of which strive to mimic natural conditions of photoperiod and temperature, more attempts have been made to understand the biology of pelage cycles in wild seals. A relationship between plasma thyroxine and plasma cortisol levels and molt has been reported in captive Pacific harbor seals (Riviere *et al.*, 1977; Engelhardt, 1977). The molt of this phocid is well-defined, occurring soon after the breeding season, and has been described for many of its subspecies (Scheffer, 1958; King, 1964; Stutz, 1967; Bishop, 1967;

Mansfield, 1967; Boulva, 1973; Riviere *et al.*, 1977). The onset of shedding is accompanied by a decrease in plasma thyroxine and increase in plasma cortisol. At completion of the molt, there is a marked increase in thyroxine and decrease in cortisol to pre-molt levels. The variation in plasma thyroxine suggests the occurrence of corresponding changes in oxygen consumption of molting seals, in accordance with known effects of thyroid hormones on basal metabolism (Hoch, 1971, 1974).

The annual molt in phocine seals occurs soon after the mating season, some species remaining out of the water for much of its duration (Freuchen, 1935; McLaren, 1958; Smith, 1973; Sergeant, 1973, Frost *et al.*, 1979; Johnson, 1979), hence feeding infrequently (McLaren, 1958; Hart and Fisher, 1964; Spalding, 1964; Johnson *et al.*, 1966; Mansfield, 1967; Hubbard, 1968; Gol'tsev, 1971). Observations of wild and captive seals suggest that the shedding period may last as long as five weeks (Scheffer and Slipp, 1944) and that it takes place first in young and subadult animals, then in adults (Scheffer and Slipp, 1944; Pitcher and Calkins, in press). Apparently seals must come out of the cold water in order to attain the behavioral, thermal, and circulatory states conducive to molting (Bullough and Rytömaa, 1964; Feltz and Fay, 1967; Fay and Ray, 1968; Ling, 1974). Elevated cortisol levels associated with the molt, which have been determined to promote lipolysis (Thompson and Lippman, 1974; Fain and Czeck, 1975), may mobilize blubber fat as an alternate energy source during this period (Engelhardt, 1979).

Pregnancy and Lactation

The energy cost of reproduction in mammals generally is estimated as the summation of energy requirements for fetal maintenance and growth, uterine maintenance, maternal work, parturition, and lactation, complicated by the concurrent needs of adult activity, maintenance, and growth if the female is not yet physically mature (Brody, 1945; Hansard and Berry, 1969). The heat production alone of a pregnant female is elevated by endocrine influences and the increased work associated with accelerated circulatory, respiratory, and excretory activities (Brody, 1945). The mammalian fetus contributes only about 2.4% to the total heat production of pregnancy, behaving metabolically as part of the maternal organism rather than as an independent homeotherm (Kleiber, Cole, and Smith, 1943; Kleiber, 1975). The mass specific energy metabolism of pregnant females is not increased until the last one-third of pregnancy when fetal growth is accelerated (Moen, 1973; Beal, 1980). In humans, this increase amounts to 15% of RMR at the end of pregnancy (Beal, 1980).

For comparative purposes among species, pregnancy has been arbitrarily divided into three parts: periods of formation and differentiation, fetal development, and fetal growth (Hansard and Berry, 1969). Fetal growth curves vary in detail between species, but generally follow an exponential pattern, reaching a maximum value for growth during late gestation (Hansard and Berry, 1969; Hafez, 1969; Rattray, 1977).

Metabolism during pregnancy has been investigated in the dog (Brody, 1945), rabbit (Pommerenke, Haney, and Meek, 1930), rat (Slonaker, 1924;

Brody, 1945; Randolph, Randolph, Mattingly, and Foster, 1977), vole (Trojan and Wojciehowska, 1967; Migula, 1969), bat (Studier, Lysengen, and O'Farrell, 1973), mouse (Myrcha *et al.*, 1969; Studier, 1979), cow (Brody, 1945), pig (Brody, 1945), and horse (Brody, 1945). In general, increased metabolism during lactation has been observed in female rats (Slonaker, 1924; Brody, 1945), bats (Studier *et al.*, 1973), mice (Myrcha, Ryszkowski, and Walkowa, 1969; Studier, 1979), voles (Migula, 1969; Kaczmariski, 1966), goats (Brody, 1945), and cattle (Brody, 1945) and has been associated with high levels of food consumption and the "work" of milk production (increased metabolic activity of mammary glands and endocrine influences on body metabolism). Measurements of fasting metabolism during lactation in some mammals reveal no change in metabolic rate over non-lactating basal levels because lactation in these species is dependent on food intake (Brody, 1945; Linzell, 1972; Moen, 1973).

Direct measurements of metabolic rate in pregnant pinnipeds have not been made, although the metabolizable energy cost of pregnancy in the harp seal has been estimated by Lavigne *et al.* (1977). Fetal growth and gestation time were incorporated into an exponential equation similar to one developed by Moen (1973) for several ungulates. Assuming an average birth weight of 7 kg, they calculated a metabolizable energy cost to the female harp seal of 2.9×10^4 kcal/fetus, or 19.22 kcal/kg fetus·day over a gestation period of 215 days. Lavigne and Stewart (1979) estimated the net production energy of a female harp seal at

whelping to be 2.54×10^4 kcal from the measured caloric density of placental tissue and an 11-kg neonate.

The energy cost of lactation in pinnipeds also has not been measured. The fat content of pinniped milk ranges from 55% in the elephant seal (LeBoeuf and Ortiz, 1977) and 53% in the grey seal (Amoroso, Goffin, Halley, Matthews, and Matthews, 1951) to 19% in the South African fur seal (Harrison, 1969), as compared to 3.7% in the cow and 4% in humans (Ben-Shaul, 1962). The fat content of Weddell seal and northern elephant seal milks increase during lactation (Stull, Brown, and Kooyman, 1967; Kooyman and Drabek, 1968; Riedman and Ortiz, 1979), while that of harp seal milk remains relatively constant (Van Horn and Baker, 1971). The major fatty acid constituents of milk fats are in the same proportions as those of the blubber (Jangaard and Ke, 1968) and appear to be derived from dietary sources (West, Burns, and Modafferi, 1979). The loss of body weight (blubber thickness) observed in nursing seals of many species suggests that feeding may be reduced or discontinued during the lactation period (Amoroso and Matthews, 1952; Laws, 1959; Sergeant, 1973; Pitcher and Calkins, in press), or that little of the assimilated food energy is used for maternal maintenance (Lavigne *et al.*, 1977). Engelhardt (1979) has measured plasma cortisol levels in lactating and pup harbor seals, noting that nursing females have higher cortisol concentrations than non-lactating females and their suckling young have lower cortisol levels than weaned pups and adults. These results agree with known effects of cortisol on lipid metabolism (Thompson and Lippman, 1974; Fain and Czeck, 1975). Where high cortisol levels promote

lipolysis, they favor breakdown of blubber fat for incorporation into milk fat; low cortisol levels, inhibiting lipolysis, permit rapid fat accumulation in a nursing pup (Engelhardt, 1979).

Lavigne *et al.* (1977) estimated the net energy cost of total milk production of a female harp seal necessary to satisfy pup energy requirements. Using an equation supplied by Moen (1973), they related total milk production (MP_T) to (1) the activity increment of a pup in kcal/day (A), (2) the daily growth increment of the pup (GI) converted to kcal (using the caloric equivalent for whole ringed seal pups of 5150 x kcal/kg: Stirling and McEwan, 1975), and (3) the average daily metabolic rate of a pup during the nursing period (M, or $2[70W_i^{3/4}]$) integrated over the number of days of lactation (n):

$$MP_T = \sum_{i=1}^n A + GI + M \quad (12)$$

The total energy cost of milk production to the female harp seal was assumed to be $1.6MP_T$ from information on dairy cattle (Crampton and Harris, 1969). For a pup growth increment of 1.6 kg/day (Templeman, 1966), $1.6MP_T$ was estimated as 3.84×10^5 kcal for the lactation period. This was equivalent to 42.7 kg of body fat, representing a 28% weight loss in a fasting 150-kg harp seal (Lavigne *et al.*, 1977).

In this study, the net energy of production for Bering Sea harbor and spotted seals was estimated from the postnatal growth of wild and captive seals, indirect measurements of body fat, changes in basal metabolism during molt, and estimates of the energy expended during pregnancy and lactation.

Methods and Materials

Postnatal Growth and Body Fat Determinations

Lacking complete information on the variation of total body weight with age in captive harbor seals from birth to physical maturity, mean weight/age data for 155 harbor seals collected at the Aleutian, Commander, and Pribilof Islands by Burns and Gol'tsev (in preparation) were separated into two growth phases (birth to sexual maturity or 0 to 4 years, and sexual maturity to old age or 5 to 24 years) by means of least squares regression of log-transformed body weight on age (Brody, 1945). Mean annual body weight for two captive spotted seals from 1 to 9 years of age were plotted and compared with growth information (length/age) obtained by Tikhomirov (1971) for Bering Sea spotted seals. A regression equation based on log-transformed body weight was developed for the birth-to-sexual maturity growth phase (0 to 3 years) from these data, and the sexual-to-physical maturity growth phase (4 to 24 years) was estimated by a regression of log-transformed M-W (or maximum body weight minus body weight at age t) on age according to the method of Brody (1945) for the range 0 to 5 years. Maximum body weight (M) was estimated from data on wild individuals (Tikhomirov, 1971) and ages 6 to 9 were excluded because they represented an experimentally-induced, constant-weight condition. Correlation coefficients were obtained for all regression lines and their significant difference from zero determined with use of Student's "t" distribution.

For both species of seals from weaning to 24 years, the net energy required for growth from one age class to the next was obtained by

multiplying the difference in body weight between successive age classes by 4240 kcal/kg, the caloric equivalent for seal tissue derived by Stirling and McEwan (1975) from studies of body composition in ringed seals. For nursing seals, the difference in body weight at weaning and at birth was multiplied by 5150 kcal/kg, the caloric equivalent for ringed seal pups (Stirling and McEwan, 1975).

Body fat contents during spring and fall of 0.3, 1, 3, 4 and 9-year-old (spring only) seals were determined indirectly by means of the tritiated water method (Holleman and Dieterich, 1973). Injection of a 10 μ Ci/kg dose of tritiated water and subsequent blood sampling were accomplished *via* catheterization of the intravertebral extrabural vein in restrained seals. Body weights were recorded prior to injection of the dose and access to water was denied the seals during the experiments. When adequate restraint was not available for very large seals, injection of dose and blood sample removal were performed epidurally with a sterile disposable 18-gauge, 3½-inch spinal needle (Becton-Dickinson) and syringe. One blood sample was removed for background radioactivity before introduction of the dose. Five-milliliter blood samples, containing 0.1 ml sodium heparin (Armour Pharmaceutical), were removed 2, 3, and 4 hours post-injection, allowing sufficient time for equilibration of the tracer with the seal's body water pool (Depocas, Hart, and Fisher, 1971; White, Cameron, and Miller, 1971). The samples were vacuum-distilled and two 1-ml aliquots were withdrawn from the distillate. Five milliliters of scintillation solution, consisting of three parts toluene to one part Triton X-100 (Packard Instrument Co.) with 5 g/l PPO and 0.1 g/l dimethyl

POPOP, were added to each aliquot. Standards were made by diluting a 10 $\mu\text{Ci/kg}$ dose for one seal to 1000 ml with distilled water and preparing aliquots in the same manner as for the blood samples. All samples were counted by a liquid scintillation system (Nuclear Chicago Mark I).

The equilibrium specific activity was determined from the plot of the logarithm of the specific activity (A) of each sample against time (t) following injection of the dose. Total body water was calculated using the relationship $TBW = I/A_0$ where I equals activity of the dose and A_0 equals equilibrium specific activity. The lean body mass was computed from the equation $LEM = TBW/0.73$ (Pace and Rathbun, 1945), where 0.73 is assumed to be the proportion of water by weight in a lean mammal. Stirling and McEwan (1975) recently determined the moisture content of fat-free tissue from ringed seal carcasses to average 71%. Fat was computed as the difference between total body weight and lean body mass.

Metabolic and Hormonal Measurements During Molt

Basal oxygen consumption in air at +20°C was measured in three postabsorptive yearling harbor seals with open-flow respirometry at two-week intervals for 2.5 months, during and after the shedding phase of the molt lasting 5.5 weeks. Immediately prior to metabolism tests, a 5-ml heparinized blood sample was collected from the intravertebral extradural vein of restrained seals as previously described. Blood samples were carefully transferred to 25-ml screw-cap glass centrifuge tubes (Kimble Glass) and centrifuged at >1500g for 15 minutes to

separate plasma from other blood constituents. One-milliliter samples of plasma from each seal were transferred to plastic sample vials (Reference Laboratory, Newbury Park, California), securely capped, and stored at -20°C overnight. Radioimmunoassays were performed for plasma thyroxine and plasma cortisol by Reference Laboratory of Newbury Park, California; thyroxine (T_4) was measured by a double radioimmunoassay technique employing a rabbit anti-thyroxine serum, a goat anti-rabbit gamma globulin, and ^{125}I labeled thyroxine as tracer; cortisol was determined with use of 1,2,6,7-H-(N)-hydrocortisone as an ^{125}I -labeled tracer and a specific rabbit anti-serum to cortisol. Mean values of BMR and plasma hormone levels were computed for each bi-weekly period. They were considered to be significantly different if $P < 0.05$ as determined by using Student's "t" test.

Determination of Reproductive Energy Expenditure

The known fetal growth and gestation time of Bering Sea harbor and spotted seals were incorporated into an estimate of the energy cost during pregnancy made by Lavigne *et al.* (1977) for harp seals. This amounted to a metabolizable energy requirement of 19.22 kcal/kg fetal weight at term day, based on an exponential equation developed for ungulates by Moen (1973). The net energy requirement was estimated by subtracting energy expended as SDA (5.5% ME) from the metabolizable energy requirement of pregnancy. Net lactation costs in these species were determined from an estimate of total milk production (MP_T) obtained

by using equation 12, and multiplied by a factor of 1.6 (Crampton and Harris, 1969; Lavigne *et al.*, 1977).

Results and Discussion

Postnatal Growth and Accumulation of Body Fat

Figure 19 presents mean weight/age data for 155 harbor seals collected at the Aleutian, Commander, and Pribilof Islands by Burns and Gol'tsev (in preparation). These data have been separated into two growth phases described by the regression equations $W = 33.3 e^{0.15t}$ ($r = 0.97$) and $W = 118.5 - 127.6 e^{-0.18t}$ ($r = -0.98$) for age classes 0 to 4 years and 5 to 24 years, respectively. The value of the correlation coefficient for each set of data caused rejection of the null hypothesis at $P = 0.05$. Mean annual body weights for two spotted seals reared in captivity from 1 to 9 years of age (Figure 20) are in close agreement with the growth data (length/age) obtained by Tikhomirov (1971) for Bering Sea spotted seals and are described by the regression equation $W = 17.3 e^{0.39t}$ ($r = 0.95$) over the age range 0 to 3 years. Mean body weights for spotted seals 4 to 24 years old were estimated from the maximum weight (M) of wild seals assumed to be physically mature (Tikhomirov, 1971) and the regression of $\ln(M-W)$ on age t for captive spotted seals 0 to 5 years old according to Brody's (1945) method.

Daily net caloric requirements for growth (daily growth increments or GI) estimated for individual harbor and spotted seals are presented in Table 20 of Chapter VII. In general, these values reflect the two-phase pattern of growth described for both species. The net energy

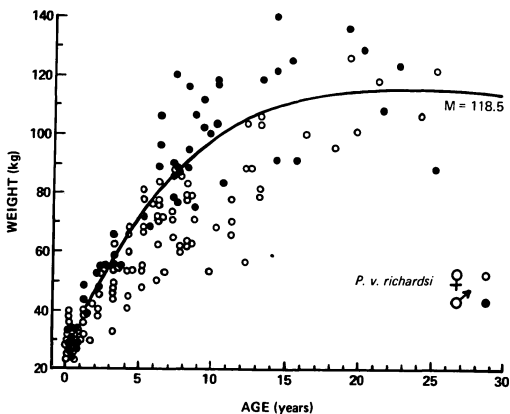


FIGURE 19. Postnatal growth (weight/age) of harbor seals from the Aleutian Ridge and Pribilof Islands, Alaska. M = maximum weight.

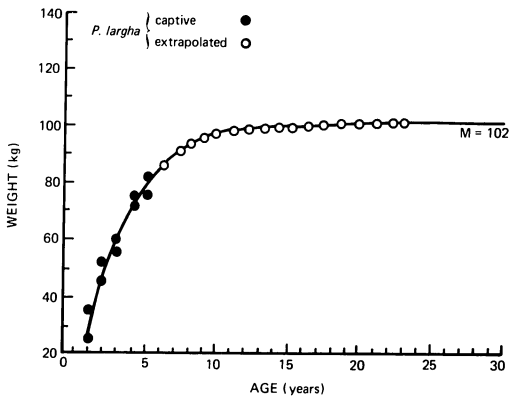


FIGURE 20. Postnatal growth (weight/age) of spotted seals derived from data on captive and wild individuals. M = maximum weight.

cost of growth is greatest for nursing pups, the weight gain of which is principally subcutaneous fat, followed by the cost of growth for seals from weaning to 1 year of age, the weight gain of which results from the development of lean mass (Bryden, 1968). Growth from 1 year onward involves further development of the lean body mass (organ size, muscle mass, and skeletal size), and net energy requirements increase gradually until the age of sexual maturity. From sexual maturity to old age, individual daily growth increments in kilocalories are described by the equation $GI = 241.7 e^{-0.18t}$ ($r = -0.99$) for harbor seals and $GI = 267.1 e^{-0.28t}$ ($r = -0.99$) for spotted seals. From sexual to physical maturity and older, the net energy requirements for growth decline as maximum skeletal size is reached. Changes in body weight beyond the age of physical maturity may reflect variation in body fat content (Curtis, 1969).

The variation of lean body mass (LBM), body fat, and total body mass (TBM) of one harbor and one spotted seal with time are shown in Figure 21. Body fat decreased from a maximum in late spring in both seals to a minimum in late summer, thereafter increasing throughout the winter. Lean body mass increased steadily with time, apparently compensating for fluctuations in body fat to produce a general trend of increasing total body mass. Variation in amount of body fat was correlated with observed seasonal variations in food intake of these seals. Both seals were in non-reproductive condition and had molted normally (the spotted seal molted in April and the harbor seal in August).

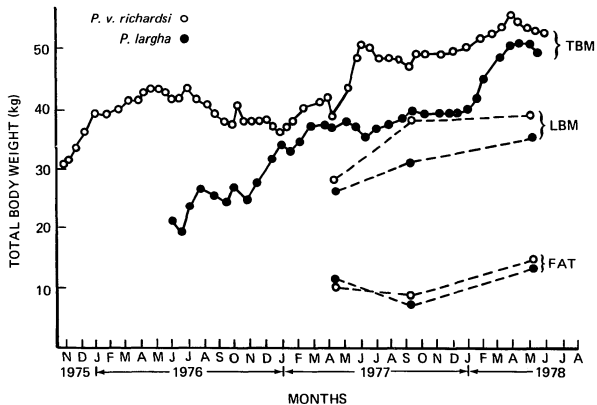


FIGURE 21. Variation of total body mass (TBM), lean body mass (LBM), and body fat (FAT) with time for one harbor and one spotted seal.

Metabolic and Hormonal Effects of Molt

Blood plasma concentrations of thyroxine and cortisol measured in three yearling harbor seals during a 5.5-week shedding phase of the molt confirmed the observations of Riviere *et al.* (1977) and Englehardt (1977, 1979). The results, plotted against time with concurrent BMR determinations (Figure 22), indicate that BMR declined to a minimum of $82 \pm 2\%$ of pre-molt levels toward the end of the molt period. The average reduction in BMR over this period was about 10% of pre-molt values. There was a high correlation between this decline and an increase in plasma cortisol ($r = -0.95$) and decrease in plasma thyroxine ($r = 0.90$), both of which commenced 2 weeks before the first observed metabolic change. Following completion of the shedding phase, metabolism gradually increased to normal levels as cortisol decreased and thyroxine increased to pre-molt values. The declines in food consumption and body fat observed during late spring to late summer in spotted and harbor seals also are related to these metabolic and hormonal changes associated with the molt; reductions in food intake and body fat content may be magnified and prolonged by the molt. Elevated cortisol levels during the molt, which have been determined to promote lipolysis, may mobilize blubber fat as an additional or alternate energy source during this period (Engelhardt, 1979). Concurrently, maintenance costs (as estimated from BMR) during molt are lower than normal, so that daily energy requirements may be met without seriously depleting body fat reserves.

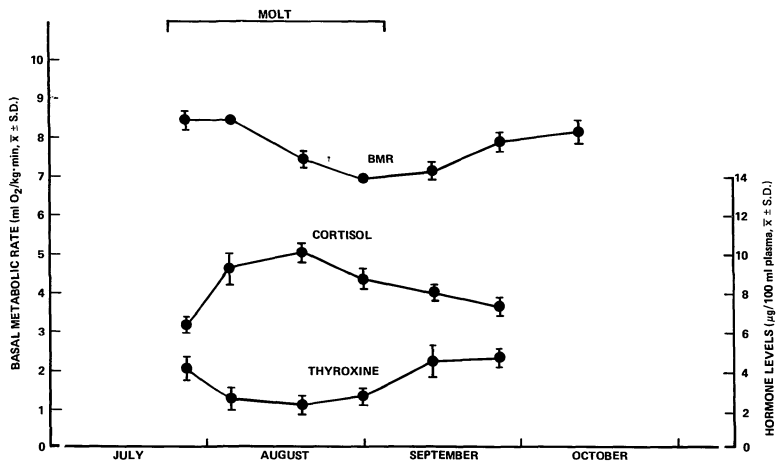


FIGURE 22. Variations in basal metabolism, plasma thyroxine, and plasma cortisol for three yearling harbor seals during the shedding phase of the molt.

Reproductive Energy Expenditure

Combined net energy costs for pregnancy and lactation in individual harbor and spotted seals, estimated according to the method of Lavigne *et al.* (1977) and Crampton and Harris (1969), were 2.4×10^5 kcal and 2.2×10^5 kcal, respectively, over a period of 280 days (252 days of pregnancy + 28 days of lactation). In harbor seals, the individual net cost of pregnancy was estimated as 5.3×10^4 kcal, comprising 22% of total reproductive energy expenditure. Individual net lactation cost in this species was estimated as 1.87×10^5 kcal, or 78% of the total cost of reproduction. In spotted seals, the estimated net cost of pregnancy per individual was 3.2×10^4 kcal, or 14% of total reproductive effort, and the estimated net cost of lactation per individual was 1.88×10^5 kcal, or 86% of total reproductive effort. Differences in pregnancy and lactation costs between these species are the result of the difference in estimated mean size of the neonate (about 12 kg in harbor seals and 7 kg in spotted seals). I have estimated that 80% of energy used for pregnancy is expended during the last 90 days in both harbor and spotted seals from fetal growth curves developed for humans, swine, and cattle (Hafez, 1969). For harbor seals this is during the spring and early summer, and for spotted seals it is in late winter.

Summary

Postnatal growth of lean tissue and body fat (total body mass) in Bering Sea harbor and spotted seals was estimated from regressions of weight/age data from captive and wild individuals and from reported

estimates of maximal body weight of wild specimens. From birth to sexual maturity, growth in harbor seals follows the derived relationship $W = 33.3 e^{0.15t}$ (0 to 4 years); in spotted seals it follows $W = 17.3 e^{0.39t}$ (0 to 3 years). From sexual to physical maturity and beyond, the growth pattern approximates the equation $W = 118.5 - 127.6 e^{-0.18t}$ (5 to 24 years) in harbor seals and $W = 102 - 95.6 e^{-0.28t}$ (4 to 24 years) in spotted seals. The net energy cost of growth is greatest for nursing seals, followed by the cost of growth for seals from weaning to 1 year of age. Subsequent energy requirements for growth are lower and increase gradually from 1 year of age to sexual maturity. From sexual to physical maturity and older, the daily individual caloric requirements for growth follow the relationship $GI = 241.7 e^{-0.18t}$ (5 to 24 years) in harbor seals and $GI = 267.1 e^{-0.28t}$ (4 to 24 years) in spotted seals. Body fat appeared to vary with season, increasing throughout fall and winter in response to cold, and decreasing from late spring to late summer as a result of the lipolytic effect of elevated cortisol and reduced BMR associated with molting. Basal metabolism of captive harbor seals was decreased by 10% during the shedding phase of the molt, preceded by a decline in plasma thyroxine and rise in plasma cortisol. All of these variables returned to pre-molt values after the end of the cycle. These observations suggest that the energy cost of new hair growth may be offset by the reduced BMR during this period. The estimated net energy costs of pregnancy and lactation for individual harbor seals are 5.3×10^4 kcal and 1.87×10^5 kcal, respectively; for individual spotted seals the costs are 3.2×10^4 kcal and 1.89×10^5

kcal, respectively. The differences between species are attributed to differing average sizes of the neonates.

CHAPTER VII
EXTRAPOLATION TO THE NATURAL POPULATION



Introduction

Few attempts have been made to estimate the energy requisites of wild pinnipeds in their natural environments. To date, energy flow has been described for populations of eastern Canadian harbor seals (Boulva, 1973), eastern Canadian ringed seals (Parsons, 1977), and western Atlantic harp seals (Lavigne *et al.*, 1977). In each study, an estimate of total energy expenditure by the population was based on a life table model incorporating information on age structure, growth, reproduction, mortality, caloric content of food and seal tissue, and food intake or metabolic rate. On the basis of his model for eastern Canadian harbor seals, Boulva (1973) estimated that 15% of gross ingested energy (GE) was lost as fecal and urinary energy (FE + UE), 79% GE was utilized as metabolizable energy (ME) for maintenance (including basal and thermoregulatory heat production and the specific dynamic action of food), and 6% GE was utilized as ME for production (including energy expended during growth and reproduction, and energy losses associated with mortality). Parsons (1977) determined that approximately 12% of the gross energy ingested by eastern Canadian ringed seals was expended as FE + UE and 88% GE was expended as ME for maintenance and production. For western Atlantic harp seals, Lavigne *et al.* (1977) calculated that 17% GE was lost as FE + UE, 80% GE was expended as ME for maintenance, and 3% GE was expended as ME for production.

In this study, the annual net and gross energy requirements of each population of Bering Sea harbor seals and spotted seals were estimated by energy flow models derived from a life table and data on the energetics

of captive individuals of each species. These estimates then were applied to the known seasonal composition and energy content of prey common to both seal species to calculate the annual consumption of each prey by both populations.

Methods and Materials

Two models were employed to estimate the annual cost of free existence for wild populations of harbor and spotted seals in the Bering Sea: Model I, based on the food consumption of captive seals (Figure 5), and Model II, based on estimates of daily metabolism per age class derived from metabolic data on resting and active seals (Table 17). Table 19 summarizes the basic assumptions and prediction equations for each model.

Mean body weights of harbor seals 0 to 24 years old were determined from data on seals collected from the Aleutian Ridge and Pribilof Islands populations by Burns and Gol'tsev (in preparation) as previously described. Mean body weights for spotted seals 0 to 3 years old were calculated from a regression of data from seals used in this study. Mean weights for spotted seals 4 to 24 years old were estimated from a regression of weight/age information on captive individuals and an estimate of the maximum weight of wild specimens (Tikhomirov, 1971). The mean body weight of the 0 age class for both species was estimated as the average weight of individuals from weaning to 1 year of age. Age frequencies based on a cohort of 1000 seals were estimated from mortality and reproductive rates for each species. Mortality and reproductive rates for harbor seals 4 to 24 years old were those estimated for the Gulf of

TABLE 19. Basic assumptions and prediction equations for Energy Flow Models I and II.

<u>MODEL I & MODEL II</u>		
1. <u>Body Weight</u>	W = weight (kg)	t = age (yrs)
	t = 0	W = 24.5 (mean value from weaning+1 yr)
	1 < t < 5	W = 33.3 e ^{0.15t} (r = 0.97)
	5 < t < 24	W = 118.5-127.6 e ^{-0.18t} (r = -0.98)
		HARBOR SEALS
	t = 0	W = 24.9 (mean value from weaning+1 yr)
	1 < t < 4	W = 17.3 e ^{0.39t} (r = 0.95)
	4 < t < 24	W = 102-95.6 e ^{-0.28t} (estimated)
		SPOTTED SEALS
2. <u>Gross Energy of Food (GE), Net Energy of Food (NE)</u>	Herring: GE = 2143 kcal kg ⁻¹ (= 12% Fat), NE = .80 GE	
3. <u>Reproductive Effort</u> = Pregnancy + Lactation Costs	= 19.22 kcal (kg fetus·day) ⁻¹ + 1.6 MP _T (see Equation 4 of text)	

MODEL I

- | | |
|-----------------------|---|
| 4. <u>Food Intake</u> | I = intake (% W) t = age (yrs) |
| | 0 < t < 24 |
| | I = 12.2 (t + 1) ^{-0.77} (r = -0.94) |

TABLE 19. Continued.

4. Continued.

MODEL II

4. Existence Metabolism (EM) = Basal Metabolism +
 Activity + Growth + Reproduction + Molt = nBMR
- | | |
|-------------------|---|
| t = Birth→Weaning | BMR = 85.5 kcal (kg day) ⁻¹ |
| t = Weaning→1 yr | BMR = 59.5 kcal (kg day) ⁻¹ |
| 1 < t < 4 | BMR = 57.5 kcal (kg day) ⁻¹ |
| 4 < t < 16 | BMR = 57.4 - 2.25t (estimated) |
| t > 16 | BMR = 70 W ^{0.75} kcal day ⁻¹ |

Alaska population by Pitcher and Calkins (in press) and mortality rates for harbor seals 0 to 3 years old were those estimated for the British Columbia population by Bigg (1969). Mortality rates for spotted seals were taken from Popov (1976). Lacking data on the reproductive maturity of spotted seals, reproductive rates for these seals were assumed to be equal to those of harbor seals.

The following assumptions were made about the steady-state characteristics of each population:

1. The age-specific reproductive, mortality, and growth rates remain constant over the range of age classes;
2. The sex ratios in each age class are even (1♂:1♀);
3. Sexual dimorphism is minimal (i.e., body weights have been averaged over both sexes);
4. The mortality in each class is natural (the population is unexploited);
5. The population is healthy (parasite loads and disease are minimal).

With Model I, the annual net caloric intake of pollock or herring was calculated for each age class from the computed mean body weight, age frequency, computed food intake (as percent body weight), and gross and net energy contents of each prey item. Since the equation used to predict food consumption was derived from data collected from seals which did not reproduce during captivity, an estimate of the caloric cost of reproductive effort was added to the food intake of all pregnant females of reproductive age, based on age-specific pregnancy rates. This

constitutes a slight over-estimate since not all of the pregnant females will carry a fetus to term; because of pup mortality, not all that give birth will experience lactation costs. The food consumption of the 0 age class was estimated as that of weaned-to-yearling pups (over a 337-day period, i.e., 365 days less lactation time), because the intake of nursing pups was accounted for by the lactation costs included in reproductive effort.

Before assessing energy requirements by Model II methods, knowledge of the diurnal activity patterns of each species is necessary to estimate the existence metabolism (EM), or average daily metabolic rate (ADMR), which is equal to the total net energy expended per day (see Equation 2). Sullivan (1979) developed a quantitative budget of daily activity for a colony of Pacific harbor seals which he observed in northern California. This activity regime was applied to Bering Sea harbor and spotted seals with some modifications to comply with known variations in behavior associated with molt, reproduction, and habitat for each species.

Table 20 presents activity budgets for several age classes of seals with estimates of net energy expenditure for each activity (in multiples of BMR) based on metabolic measurements and estimates. This table was used to calculate the daily net energy requirements of populations of harbor and spotted seals. It was assumed that spotted seals spend more time in water than harbor seals (60 *versus* 56%) during the non-reproductive and non-molting seasons, based on observations that they are more migratory and less gregarious than harbor seals (Burns, 1970; Burns *et al.*, 1972; Fay, 1974; Shaughnessy and Fay, 1977). During the pupping

TABLE 20. Estimated daily activity patterns and net cost of activity for Bering Sea harbor and spotted seals in relation to molt, reproduction and other periods. B = birth, W = weaning.

Activity	PERCENT OF DAY AND NET ENERGY COST (n BMR)					
	Harbor Seals			Spotted Seals		
	B - 1 yr	1 - 24 yrs		B - W	W - 24 yrs	
Molt		Other	Molt		Repro.	Other
<u>Water</u>						
Swimming, diving	60.3 (1.6)	30 (1.35)	56 (1.5)	Assume	30 (1.35)	56 (1.5)
Sleeping	9.7 (0.8:B-W) (0.7:W-1)	---	---	activity =	---	9.7 (0.7)
<u>Land</u>						
Alert behavior	3.7 (1.3)	8.6 (1.17)	5.4 (1.3)	land activ-	8.6 (1.17)	5.4 (1.3)
Locomotion	3.6 (1.7)	8.4 (1.53)	5.3 (1.7)	ity and NE	8.4 (1.53)	5.3 (1.7)
Comfort behavior	1.3 (1.2)	3.2 (1.08)	2.0 (1.2)	cost	3.2 (1.08)	2.0 (1.2)
Agonistic behavior	0.6 (2.1)	1.3 (1.89)	0.8 (2.1)	= BMR	1.3 (1.89)	0.8 (2.1)
Sleeping	20.8 (0.8:B-W) (0.7:W-1)	48.5 (0.7)	30.5 (0.7)		48.5 (0.7)	30.5 (0.7)
Growth increment	2354.3 (B-W)	72.0 (1 yr)		3273.9	8.8 (W-1 yr)	
GI (kcal day ⁻¹)	178.6 (W-1)	84.8 (2 yrs) 98.7 (3 yrs) 68.5 (4 yrs) GI = 241.7 e ^{-0.18t} (5 yrs ≤ t < 24 yrs)			140.5 (1 yr) 209.0 (2 yrs) 175.4 (3 yrs) GI = 267.1 e ^{-0.28t} (4 yrs ≤ t < 24 yrs)	
Reproductive Effort (kcal) over 280 days	0	2.4 × 10 ⁵ (4-24 yrs)		0	2.2 × 10 ⁵ (4-24 yrs)	

and mating seasons, adult spotted seals form widely separated pairs at the ice front for about 2 months (Burns *et al.*, 1972; Fay, 1974). On this basis, it was assumed that non-aquatic activity in this species at that time was equal to that exhibited by harbor seals during their reproductive season (44%). From the observations of Sullivan (1979) and others (Bishop, 1967; Wilson, 1974a, 1974b), it was assumed that harbor seal pups are active after birth, spending more time in water than subadults and adults (70 *versus* 56%). Spotted seal pups are reported to be quite sedentary following birth, becoming aquatic when the lanugo is shed at weaning (Burns, 1970; Naito and Nishiwaki, 1972). Thus, they were assumed to require energy primarily for basal metabolism until weaning, after which their activity levels and energy requirements were considered equivalent to those of harbor seal pups. It was assumed that members of both species remain out of water during the molt from observations of harbor seals during this period (Johnson and Johnson, 1979). The proportion of time allotted for each behavior exhibited by seals on land was kept constant in each activity budget estimated for reproduction, molting, and other seasons.

Prediction equations for annual growth increments in harbor and spotted seals for use with Model II also are presented in Table 20 and were derived from postnatal growth equations as previously described. Beyond the age of physical maturity when growth of lean tissue essentially ceases (Curtis, 1969), the estimated caloric value of seal tissue, 4240 kcal/kg (Stirling and McEwan, 1975), may be greater because further

weight gain would be attributable to fat deposition. Therefore, annual growth increments for seals beyond age 15 may be under-estimated.

Results and Discussion

The annual net energy requirements of each cohort of 1000 seals, as predicted by both models, are shown in Tables 21 and 22. The close agreement between net energy requirements for age classes 2 to 24 predicted by Models I and II reflects a high correlation of food intake with metabolic data for captive seals ($r = 0.97$). Large differences between the two models for age classes 0 and 1 may be a consequence of greater activity and food intake by captive young seals of both species than by wild individuals, as influenced by training and adjustment to captivity.

Based on the means of the predicted net energy requirements as best estimates for each class, approximately 40% of the total annual net energy required by each population is necessary to sustain the 0 to 3-year-old age classes in harbor and spotted seals. This is a result of the higher growth rates, greater abundance, and higher basal metabolism of younger seals as compared to older animals. Approximately 94% of the total annual net energy requirement of each population is expended for maintenance (basal metabolism, thermoregulation, and activity) and 6% for production (growth and reproduction). That component of net energy necessary for growth in both species comprises more than 50% of the total annual net energy requirement of the age class in newborn to weanling seals, 2 to 7% in weanling to 3-year-old seals, and less than 2%

TABLE 21. Energy flow table for a cohort of 1000 Bering Sea harbor seals.

Age (yrs)	Wt (kg)	Age Freq.	Biomass (kg)	Mort. Rate	Biomass Dead (kg)	Preg. Rate	Freq. Preg.	Mean Daily Net Energy Requirement (kcal x 10 ⁵)		Annual Net Energy Requirement (kcal x 10 ⁷)	
								Model I	Model II	Model I	Model II
0	24.5	149.1	3653.0	.23	840.2	0	0	7.65	3.10	25.81	10.48
1	38.7	114.8	4523.1	.20	904.6	0	0	5.50	3.22	20.08	11.78
2	44.9	91.8	4121.8	.17	700.7	0	0	3.67	2.99	13.43	10.94
3	52.2	76.2	3893.8	.17	661.9	0	0	2.87	2.89	10.48	10.56
4	60.7	63.2	3678.2	.11	404.6	.17	5.4	2.34	2.36	8.56	8.05
5	66.6	56.2	3726.1	.10	372.6	.63	17.7	2.11	2.30	7.71	8.40
6	75.2	50.6	3820.3	.10	382.0	.88	22.3	1.91	2.25	6.99	8.23
7	82.3	45.5	3744.7	.09	337.0	.89	20.2	1.74	2.08	6.36	7.61
8	88.3	41.4	3655.6	.09	329.0	1.00	20.7	1.52	1.93	5.55	7.66
9	93.2	37.7	3513.6	.09	316.2	.88	16.6	1.38	1.73	5.05	6.35
10	97.4	34.3	3340.8	.09	300.7	.79	13.5	1.18	1.53	4.31	5.62
11	100.9	31.2	3148.1	.09	283.3	.97	15.1	1.07	1.37	3.92	5.03
12	103.8	28.4	2947.9	.09	265.3	.97	13.8	0.95	1.20	3.48	4.39
13	106.2	25.8	2740.0	.08	219.2	.97	12.5	0.83	1.03	3.05	3.79
14	108.2	23.7	2564.3	.09	230.8	.97	11.5	0.73	0.89	2.69	3.28
15	109.9	21.6	2373.8	.10	237.4	.97	10.5	0.64	0.76	2.34	2.80
16	111.3	19.4	2159.2	.10	215.9	.94	9.1	0.58	.65	2.12	2.38
17	112.5	17.5	1968.8	.11	216.6	.94	8.2	0.52	0.57	1.93	2.11
18	113.5	15.6	1770.6	.10	177.1	.94	7.3	0.47	0.51	1.73	1.89
19	114.3	14.0	1600.2	.13	208.0	.94	6.6	0.42	0.46	1.56	1.71
20	115.0	12.2	1403.0	.12	168.4	.94	5.7	0.37	0.40	1.37	1.49
21	115.6	10.7	1236.9	.15	185.5	1.00	5.4	0.33	0.36	1.23	1.33
22	116.1	9.1	1056.5	.14	147.9	1.00	4.6	0.28	0.30	1.03	1.13
23	116.5	7.8	908.7	.82	745.1	1.00	3.9	0.24	0.26	0.89	0.97
>23	118.5	1.4	165	1.00	165.9	1.00	0.7	0.04	0.49	0.16	0.18
Totals		1000.0	67714.9		9015.9		231.3	39.34	35.63	141.83	128.16

TABLE 22. Energy flow table for a cohort of 1000 Bering Sea spotted seals.

Age (yrs)	Wt (kg)	Age Freq.	Biomass (kg)	Mort. Rate	Biomass Dead (kg)	Preg. Rate	Freq. Preg.	Mean Daily Net Energy Requirement (kcal x 10 ⁵)		Annual Net Energy Requirement (kcal x 10 ⁷)	
								Model I	Model II	Model I	Model II
0	24.9	149.1	3712.6	.23	853.9	0	0	7.79	2.80	26.25	9.44
1	25.6	114.8	2938.9	.20	587.8	0	0	3.63	2.32	13.25	8.48
2	37.7	91.8	3460.9	.17	588.4	0	0	3.09	2.74	11.28	10.01
3	55.7	76.2	4244.3	.17	721.5	0	0	3.06	3.25	11.17	11.89
4	70.8	63.2	4474.6	.11	492.2	.17	5.4	2.72	2.75	9.94	10.07
5	78.4	56.2	4406.1	.10	440.6	.63	17.7	2.45	2.65	8.97	9.68
6	84.2	50.6	4260.5	.10	426.1	.88	22.3	2.10	2.46	7.68	9.00
7	88.5	45.5	4026.8	.09	362.4	.89	20.2	1.85	2.21	6.75	8.07
8	91.8	41.4	3800.5	.09	342.0	1.00	20.7	1.55	1.98	5.68	7.23
9	94.3	37.7	3555.1	.09	320.0	.88	16.6	1.38	1.73	5.04	6.35
10	96.2	34.3	3299.7	.09	297.0	.79	13.5	1.15	1.50	4.21	5.50
11	97.6	31.2	3045.1	.09	274.1	.97	15.1	1.03	1.32	3.76	4.82
12	98.7	28.4	2803.1	.09	252.3	.97	13.8	0.90	1.13	3.29	4.15
13	99.5	25.8	2567.1	.08	205.4	.97	12.5	0.78	0.96	2.87	3.53
14	100.1	23.7	2372.4	.09	213.5	.97	11.5	0.67	0.83	2.48	3.03
15	100.6	21.6	2172.9	.10	217.3	.97	10.5	0.58	0.70	2.13	2.55
16	100.9	19.4	1957.5	.10	195.8	.94	9.1	0.52	0.59	1.92	2.14
17	101.2	17.5	1771.0	.11	194.8	.94	8.2	0.47	0.53	1.75	1.95
18	101.4	15.6	1581.8	.10	158.2	.94	7.3	0.42	0.48	1.55	1.74
19	101.5	14.0	1421.0	.13	184.7	.94	6.6	0.38	0.43	1.39	1.56
20	101.6	12.2	1239.5	.12	148.7	.94	5.7	0.33	0.37	1.23	1.36
21	101.7	10.7	1088.2	.15	163.2	1.00	5.4	0.29	0.33	1.07	1.09
22	101.8	9.1	926.4	.14	129.7	1.00	4.6	0.24	0.28	0.90	1.02
23	101.9	7.8	794.8	.82	651.7	1.00	3.9	0.21	0.24	0.78	0.87
>23	102.0	1.4	142.8	1.00	142.8	1.00	0.7	0.04	0.04	0.13	0.16
Totals		1000.0	66063.6		8564.1		231.3	37.63	34.62	135.47	126.00

in seals 4 to 24 years old. Individual pregnant and lactating seals of both species require about 13% or more net energy per year than non-reproducing females and males. The fraction of NE for an individual seal represented by reproductive effort possibly increases with age because of decreasing basal metabolism.

Table 23 presents estimates of the proximate composition of four prey important in the diets of the seals and the percentage of the seals' annual gross energy requirement represented by each prey. Available data on seasonal food habits suggests that these species may provide a major portion of the annual gross energy requirement of both seal populations and rank in importance to the seals' overall diet as shown in the table. Negligible intake of other prey and negligible variation of food habits with age have been assumed in order to simplify the computations. Present evidence suggests that other prey are taken and that younger animals may consume more invertebrates and small finfish than older seals (Pitcher and Calkins, in press; K. Frost, personal communication). Variation of fat content in capelin (*Mallotus villosus*) and herring is attributed to fat loss while fasting during spawning migrations in late spring and early summer, with fat replenishment during vigorous feeding after spawning (Stoddard, 1968; MacCallum *et al.*, 1969; Jangaard, 1974). Annual mean energy values indicative of this trend have been used to estimate seasonal consumption of capelin and herring by the seals.

The seasonal and annual consumption of each kind of prey in metric tons by both seal populations is presented in Table 24. The annual net

TABLE 23. Estimated percent of total gross energy required and proximate composition of four important prey in the diets of Bering Sea harbor and spotted seals. S = spring and summer; W = fall and winter

Species	% Gross Energy Requirement of Seals		Proximate Composition of Food					Reference
	S	W	% H ₂ O	% Protein	% Fat	% Ash	Energy (kcal/kg wet)	
Pollock <i>Theragra chalcogramma</i>	10.0	20.0	78.8	19.2	0.8	1.6	1088	This study
Capelin <i>Mallotus villosus</i>	20.0	10.0	77.1-82.3	12.9-15.0	8.1-1.8	-	\bar{x} = 2177*	MacCallum <i>et al.</i> , 1969; (spawning capelin)
	-	-	-	12.3-15.0	23.4-6.5	-	\bar{x} = 2177*	Jangaard, 1974 (feeding capelin)
Herring <i>Clupea harengus pallasi</i>	15.0	10.0	64.0-71.7	16.3-20.0	18.0-5.1	2.0-2.4	2418-1564	This study
Invertebrates (Cephalopods, crustaceans)	5.0	10.0	79.9-80.2	12.5-17.8	1.4-0.9	1.4-2.2	\bar{x} = 964*	Geraci, 1975

* Calculated from proximate composition data.

TABLE 24. Estimated seasonal gross energy requirements and intake of four important prey by Bering Sea harbor and spotted seals. S = spring and summer; W = fall and winter.

Species	Population		Gross Energy		Prey Intake (metric tons x 10 ³)							
	(x 10 ⁵)		(kcal x 10 ¹⁰)		Pollock		Capelin		Herring		Invertebrates	
	S	W	S	W	S	W	S	W	S	W	S	W
Harbor seal	1.5	1.5	12.6	12.6	11.6	23.1	20.2	5.8	12.1	5.9	6.5	13.1
Spotted seal	1.25	2.5	10.2	20.4	9.4	37.5	16.3	9.4	9.8	9.5	5.3	21.2
Total/Season					21.0	60.6	36.5	15.2	21.9	15.4	11.8	34.3
Total/Year					81.6		51.7		37.3		46.1	

energy requirements computed from Models I and II for 1000 seals in each life table were averaged for each species, divided equally between two general seasons (spring and summer, fall and winter), and extrapolated to the seasonal populations of Bering Sea harbor and spotted seals as estimated by McAlister *et al.* (1976). The total net energy requirement per season (NE_T) for each seal population was then converted to total gross energy (GE_T) using the net energy coefficient:

$$\frac{NE_T}{.80} = GE_T \quad (13)$$

The fraction of the gross energy represented by each prey (GE_i) was then converted to metric tons consumed (I) with use of the appropriate seasonal caloric content (E) as in the following example:

Capelin - Harbor Seal Diet

$$\begin{aligned} \text{Spring and Summer: } I &= \frac{GE_i}{E} = \frac{25.2 \times 10^9 \text{ kcal}}{1.25 \times 10^3 \text{ kcal/kg}} = 20.2 \times 10^3 \text{ m.t.} \\ \text{Fall and Winter: } I &= \frac{GE_i}{E} = \frac{12.6 \times 10^9 \text{ kcal}}{2.18 \times 10^3 \text{ kcal/kg}} = 5.8 \times 10^3 \text{ m.t.} \end{aligned} \quad (14)$$

Comparison of annual consumption data for pollock and herring from Table 24 with recent commercial fishery statistics (Pereyra *et al.*, 1976; National Marine Fisheries Service, 1977) suggests that the pollock and herring intake of the total number of Bering Sea harbor and spotted seals may be about 9 and 20%, respectively, of the commercial take.

The ecological efficiency of each seal species was calculated according to the definition of Slobodkin (1960) for a steady-state population where yield is equal to production for any given time period:

$$\text{Ecological Efficiency} = \frac{\text{Yield}}{\text{Ingestion}} \times 100\% \quad (15)$$

Yield was computed as the annual biomass of dead seals for each population, converted to kilocalories using the caloric equivalent for seal tissue (4240 kcal/kg) derived by Stirling and McEwan (1975). Ingestion was equivalent to the annual gross energy required by each population in kilocalories. Ecological efficiency in Bering Sea harbor seals was 2.27% and in spotted seals was 2.23%. These efficiency values are nearly identical and are consistent with those obtained for harp seal (Lavigne *et al.*, '977) and ringed seal (Parsons, 1977) populations using similar energy budget models, and are in agreement with predicted results for homeotherms (Turner, 1970; Steele, 1974).

Summary

The combined seasonal net energy requirements of Bering Sea harbor seals and spotted seals, estimated by application of life table models to data on the energetics of captive seals and extrapolated to the seasonal populations of each species, were 1.83×10^{11} kcal in summer and 2.65×10^{11} kcal in winter. These values, when converted to the annual gross energy requirement of each population and applied to data on seasonal consumption and caloric content of important prey, corresponded to an annual intake of 8.16×10^4 metric tons of pollock, 5.17×10^4 metric tons of capelin, 3.73×10^4 metric tons of herring, and 4.61×10^{11} metric tons of invertebrate species. These estimates suggest that the annual pollock and herring consumption of both seal populations may be about 9% and 20% respectively, of the present commercial take of these fishes.

The calculated ecological efficiency of each seal population, 2.27% for harbor seals and 2.23% for spotted seals, is consistent with values predicted for other mammals.

CHAPTER VIII

GENERAL SUMMARY

The daily net energy expenditures of several captive Bering Sea harbor seals (*Phoca vitulina richardsi*) and spotted seals (*Phoca largha*) were estimated from long-term studies of food intake and proximate composition, food energy content and digestibility, and metabolic effects of temperature, feeding, exercise, molt, and reproduction. Energy flow models based on these estimates were developed and applied to a life table for the Bering Sea population of each species to approximate its annual net energy expenditure in its natural environment. The seasonal and annual gross energy requirements of harbor and spotted seals were estimated from their mean annual net energy expenditure and from the caloric values of representative prey foods eaten by each seal species during the year. The total wet weight consumption of pollock (*Theragra chalcogramma*) and herring (*Clupea harengus pallasii*), two important finfish in terms of volume in the diets of these seals, was derived from the gross caloric intake of these fishes by the seals and related to the present catch statistics of each commercial fishery in the Bering Sea.

Proximate Composition, Gross Energy, and Consumption of Food

Pollock and herring were used in nutritional studies with captive Bering Sea harbor and spotted seals. The gross energy (GE) or caloric value of pollock and herring varied directly with fat content and indirectly with moisture content. Significant differences between water,

protein, and lipid contents of separate lots of herring were attributed to possible seasonal, environmental, and physiological factors affecting the nutritional state of the catch. Captive harbor and spotted seals were able to obtain their caloric requirements from herring diets of varying energy content by adjusting their food intake during *ad libitum* feeding. Captive yearling and subadult seals consumed more food in winter than in summer, regardless of its energy content. The food consumption of wild harbor and spotted seals was approximated by the equation $y = 12.2 (x + 1)^{-0.77}$ ($r = -0.95$), based on the food intake of two captive spotted seals from ages 1 to 9 years, where y equals percent body weight consumed and x equals age in years.

Digestible Energy

Captive Bering Sea harbor seals, and pinnipeds in general, are able to digest at least 90% of the gross energy of ingested food. In yearling and subadult harbor seals, the mean digestible energy (DE) of herring was $91.2 \pm 0.7\%$ of gross ingested energy. In subadult harbor seals, the mean digestibility of pollock, $96.7 \pm 0.2\%$ GE, was significantly different from that of herring ($P < 0.001$). This was attributed to slower passage of pollock through the gut of these seals as compared with herring. In general, a more rapid passage of digesta through the gut of pinnipeds than other large carnivores was indicated by the transit times, clearance rates, and gastrointestinal turnover times measured for pollock and herring in captive harbor seals.

Nitrogen-Corrected Metabolizable Energy

Captive yearling and subadult harbor seals exhibited a positive nitrogen balance or nitrogen retention on a herring diet, indicating daily growth or protein gain. Yearling seals fed herring retained significantly more nitrogen per kilogram of body weight than subadult seals fed herring or pollock ($P < 0.05$) as a requirement for more rapid body growth. A significantly greater amount of nitrogen was retained by subadult seals on a pollock diet than on a herring diet ($P < 0.05$) because of the greater quantity and digestibility of protein in pollock. Nitrogen-corrected metabolizable energy (ME_n) values of 85.3% GE and 83.7% GE were estimated for yearling and subadult seals, respectively, fed maintenance rations of herring. Subadult seals fed maintenance rations of pollock had an ME_n value of 85.9% GE because of greater nitrogen retention.

Specific Dynamic Action and Net Energy

The specific dynamic action of food (SDA) exhibited by captive harbor seals fed maintenance rations of herring was comparable to SDA measurements in other mammals fed high-protein diets when expressed as a percent increase in basal metabolism. The SDA of herring fed at maintenance levels to yearling harbor seals was 5.5% ME, or 4.7% GE, and it increased at higher levels of food intake and decreased with sleep. A value of 292.9 cal/g dry food was assumed to be a reasonable estimate of SDA for harbor and spotted seals fed herring or pollock. The net energy

(NE), or difference between nitrogen-corrected metabolizable energy and SDA, was estimated at 80.3% GE for a herring or pollock diet.

Net Energy for Maintenance

The net energy requirement for maintenance (NE_m) in captive harbor and spotted seals was estimated from measurements of metabolic rate during rest, activity, sleep, and thermoregulation. Basal metabolic rate in harbor and spotted seals 0.2 to 9 years old declined from 2.4 to 1.5 times predicted values for terrestrial mammals of equivalent weight. In air and water temperatures typical of the Bering Sea, BMR was sufficient to maintain thermal homeostasis. The daily energy cost for normal physical activity was lower in captive harbor and spotted seals than for similar activity in other mammals. Energy was conserved during sleeping and diving, with a range of expenditure from 60 to 90% BMR during sleeping and 91 to 96% BMR during diving. The metabolic scope for activity measured in captive yearling harbor seals was approximately 4BMR, which also is low in comparison with the metabolic capacities of other large terrestrial mammals but similar to those of sea otters and small rodents.

Net Energy for Production

The net energy requirement for production (NE_p) in harbor and spotted seals was estimated from data on the postnatal growth and seasonal variation in body fat of wild and captive seals, the caloric value of seal tissue, the metabolic rates of captive seals during molting, and the estimated energy costs of pregnancy and lactation.

In general, the net energy required for growth in seals from birth to sexual maturity was a larger fraction of the total net energy cost of production than in sexually mature and older seals. From sexual to physical maturity and older, the individual daily caloric requirements for growth (GI) followed the relationship $GI = 241.7 e^{-0.18t}$ ($r = -0.99$) in harbor seals and $GI = 267.1 e^{-0.28t}$ ($r = -0.99$) in spotted seals where t equals age in years.

The net energy cost of new hair growth for harbor seals was offset by a 10% reduction in basal energy requirements during the shedding phase of the molt. During a 5.5-week period, the BMR of captive yearling harbor seals declined to a minimum of $82 \pm 2\%$ of pre-molt levels, preceded by a decline in plasma thyroxine and rise in plasma cortisol. After the end of the shedding phase, all of these variables returned to pre-molt values. Declines in food consumption and body fat observed during late spring to late summer in spotted and harbor seals may be a response to higher ambient temperatures and to the lipolytic effect of elevated cortisol levels and reduced daily energy requirements associated with molting.

The estimated net energy costs of pregnancy and lactation for individual harbor seals were 5.3×10^4 kcal and 1.87×10^5 kcal, respectively, and for spotted seals were 3.2×10^4 kcal and 1.88×10^5 kcal, respectively. The differences between species resulted from differing average sizes of neonates used in the calculations.

The Energy Cost of Free Existence for Bering Sea Harbor and Spotted Seals

The combined gross energy requirements of harbor and spotted seals, estimated from energy flow models and extrapolated to the seasonal populations of each species in the Bering Sea, were 2.28×10^{11} kcal in summer and 3.30×10^{11} kcal in winter. The difference in seasonal gross energy values resulted from the assumption that a greater number of spotted seals are present in winter than in summer. The annual gross energy requirement of both populations, 5.60×10^{11} kcal, when applied to data on feeding habits and energy content of important prey, corresponded to an annual consumption of 8.16×10^4 metric tons of pollock, 5.17×10^4 metric tons of capelin, 3.73×10^4 metric tons of herring, and 4.61×10^4 metric tons of invertebrate species. Based on these estimates, the annual pollock and herring intake of both seal populations may be about 9% and 20%, respectively, of the present commercial take of these fishes.

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