SEASONAL CHANGES IN THE ENERGY BUDGETS OF CAPTIVE HARBOUR SEALS (PHOCA VITULINA CONCOLOR)

DAVID A.S. ROSEN

SEASONAL CHANGES IN THE ENERGY BUDGETS OF CAPTIVE HARBOUR SEALS (*PHOCA VITULINA CONCOLOR*)

by

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Radiation	0821
Veterinary Science	0778
Zoology	0472
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Geodesy	0370
Geology	0372
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Hydrology	0388
Mineralogy	0411
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Paleoecology	0426
Paleontology	0418
Paleozoology	0985
Palynology	0427
Physical Geography	0368
Physical Oceanography	0415

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Human Development	0758
Immunology	0982
Medicine and Surgery	0564
Mental Health	0347
Nursing	0569
Nutrition	0570
Obstetrics and Gynecology	0380
Occupational Health and Therapy	0354
Ophthalmology	0381
Pathology	0571
Pharmacology	0419
Pharmacy	0572
Physical Therapy	0382
Public Health	0573
Radiology	0574
Recreation	0575
Speech Pathology	0460
Toxicology	0383
Home Economics	0386

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Biochemistry	0487
Inorganic	0488
Nuclear	0738
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Pharmaceutical	0491
Physical	0494
Polymer	0495
Radiation	0754
Mathematics	0405
Physics	
General	0605
Acoustics	0986
Astronomy and Astrophysics	0606
Atmospheric Science	0608
Atomic	0748
Electronics and Electricity	0607
Elementary Particles and High Energy	0798
Fluid and Plasma	0759
Molecular	0609
Nuclear	0610
Optics	0752
Radiation	0756
Solid State	0611
Statistics	0463

Applied Sciences

Applied Mechanics	0346
Computer Science	0984
Engineering	
General	0537
Aerospace	0538
Agricultural	0539
Automotive	0540
Biomedical	0541
Chemical	0542
Civil	0543
Electronics and Electrical	0544
Heat and Thermodynamics	0348
Hydraulic	0545
Industrial	0546
Marine	0547
Materials Science	0794
Mechanical	0548
Metallurgy	0743
Mining	0551
Nuclear	0552
Packaging	0549
Petroleum	0765
Sanitary and Municipal	0554
System Science	0790
Geotechnology	0428
Operations Research	0796
Plastics Technology	0795
Textile Technology	0994

PSYCHOLOGY

General	0621
Behavioral	0384
Clinical	0622
Developmental	0620
Experimental	0623
Industrial	0624
Personality	0625
Physiological	0989
Psychobiology	0349
Psychometrics	0632
Social	0451

Abstract

Seasonal changes in several components of the energy budgets of captive harbour seals (*Phoca vitulina concolor*) were studied to further understand previously documented cycles of energy conservation and utilization. Body mass in adult seals varied by 16-30% (15-32 kg) throughout the year, resulting in net production energy of ±200 MJ/week. Circannual variation in gross energy intake (GE) resulted in a range of 30-300 MJ/week. Combined, concurrent changes in GE and body mass resulted in a range in available energy (EA) of 50-350 MJ/week. Resting metabolic rate (RMR) displayed significant seasonal variation (45-129 MJ/week), and accounted for 10-90% of EA throughout the year. Changes in RMR may serve as either an adaptation or a response to varying levels of energy turnover. Mass-specific metabolism exhibited a stronger statistical relationship to EA than did RMR. Locomotor activity was significantly related to EA for all the male seals, but not for the female. The strength of the statistical relationship in the mature males derived largely from the high levels of activity and EA during the breeding season. However, increases in locomotor activity could not account for all of the observed EA. Rectal temperatures, which displayed a circannual variation of 2.0-2.8°C, were related to EA for only three of the seals and were more closely related to water temperature. The observed variation in core temperature was speculated to result from changes in deep body set-points. The substantial changes that were documented to occur throughout the year in many aspects of the seals' energy budgets highlight the need for long-term investigations of energetics, metabolic physiology and feeding ecology.

Acknowledgments

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Table of Contents

List of Tables

List of Figures

Pages

Chapter 1 - Introduction

Research into seasonal variation in the energy budgets of mammals has concentrated largely upon two overlapping groups: those which undergo hibernation or torpor and those living in polar or subpolar climes. Research on the former has concentrated on seasonal depressions in metabolism and deep body temperatures, while research on the latter group has concentrated on the physical and behavioural adaptations to a highly seasonal food supply.

Pinnipeds possess characteristics of both of these groups. Although seals are recognized for their capacity for physiological adaptation to extreme environmental demands, seasonal variation in the energetics of pinnipeds has been largely unstudied. Pinnipeds in the wild are usually only readily accessible for study during the brief breeding and moulting periods, when they are more reliant on terrestrial or ice substrates. Therefore, field studies are restricted in their ability to investigate seasonal changes.

Seasonal changes in body mass and food intake have been documented previously in a group of captive harbour seals. Renouf & Noseworthy (1990; 1991) found that, contrary to initial expectations, the seals lost mass during periods of hyperphagia and gained mass during periods of hypophagia. This unusual, and initially controversial, result suggested three hypotheses. First, seasonal changes in body mass were not the direct result of changes in food intake. Second, harbour seals underwent periods of high energy utilization and conservation. Third, the observed seasonal variations in body mass were the result of a shift in some other component(s) of the seals' energy budgets during the course of the year. However, the specific nature or source of these hypothesized changes was unknown.

The present study documents circannual changes in body mass and energy intake in a group of captive harbour seals in order to quantify changes in energy utilization throughout the year. The energy derived from food intake and changes in body mass constitute the majority of the energy available to subsequent bioenergetic pathways. This study documents circannual variation in several components of the seals' energy budgets to determine which avenues account for the changes in available energy, concentrating on those bioenergetic parameters most likely to reflect and/or facilitate such changes. As a guideline, Kleiber (1975) proposed that there were four avenues by which homeotherms may reduce their energy expenditure: 1) reduction of metabolic rate; 2) avoidance of the need for increased heat production due to low temperatures; 3) reduction of locomotor activity; and 4) avoidance of energy-requiring processes, such as reproduction and growth.

Previous studies have indicated that the metabolic rates of phocid seals display significant adaptability to variation in food supplies (Ashwell-Erickson & Elsner 1981; Ashwell-Erickson *et al.* 1986; Castellini & Rea 1992; Rea & Costa 1992; Worthy *et al.* 1992; Markussen *et al.* 1992b; Nordøy *et al.* 1993a). Therefore, it was proposed that metabolism among the captive harbour seals should undergo seasonal changes to facilitate shifts in energy utilization. Past studies also indicate that the rectal temperatures of phocids are variable, displaying both a circadian rhythm and short-term changes related to behaviour (Bartholomew 1954; Whittow *et al.* 1971; Ohata *et al.* 1972; Whittow 1987; Hokkanen 1990). Assuming a physiological link between body temperature and metabolic rates, it was predicted that changes in energy utilization should produce parallel changes in rectal temperatures. In addition, given the seasonal nature of their social behaviour (Thompson *et al.* 1989; Renouf & Noseworthy 1990), it was also predicted that the observed shifts in the seals' energy budgets were related to changes in activity levels.

The current study is unique in that it traces long-term, longitudinal changes in several physiological parameters. The aim of the study was not only to document seasonal variation in these factors, but to relate and quantify their relative influence on annual energy budgets. A bioenergetic framework was utilized to compare variables along a common currency and to quantify the effects of the observed seasonal changes on the seals' energy budgets.

Such an approach necessitated several methodological changes from past research. This study documents seasonal changes in gross energy intake rather than food mass intake, as it has been suggested that some of the variation observed in food intake in past studies was the result of changes in the energy density of the food. It also examines the steps involved in the conversion of gross energy intake to net energy, and the range of estimates for these variables. As in Renouf & Noseworthy's (1990; 1991) studies, seasonal variation in body mass was measured, but the current study also used body composition data to estimate the energetic significance of these changes.

Accurate estimates of the extent and pattern of seasonal variation in the energy budgets of individuals are important for two reasons. First, documenting concurrent changes in several components of the energy budgets leads to a better understanding of their interaction and adaptive significance. Second, recognizing the effects of seasonal variation is important when constructing models of population energetics. Most marine mammal energetics models use parameter estimates gathered over short intervals, applied uniformly across the yea (Härkönen & Heide-Jørgensen 1991; Markussen & Øritsland 1991; Markussen *et al.* 1992a; Lockyer 1993; Olesiuk 1993). Failing to recognize possible seasonal variation can lead to two sources of error. First, prey consumption is incorrectly assumed to be evenly distributed throughout the year. Second, biased estimates of energetic parameters will result if measures are taken at a time of the year non-representative of annual means.

This study estimates variation in the energy made available from food intake and changes in body mass. It documents the extent of seasonal variation within several components of the harbour seal's energy budget, and examines which components account for the variation in available energy. It provides mathematical descriptions of circannual variation in these components, including estimates of the strength of these formulae. Finally, it discusses the effect that seasonal variation may have upon models of marine mammal population energetics.

Chapter 2 - Method

Study Animals:

The study group consisted of six captive Atlantic harbour seals (*Phoca vitulina concolor*), five males, hereafter referred to as males #1-5, and one female. Males #1-4 were born in 1972, 1978, 1985, and 1986, respectively, making them 19, 13, 6, and 5 years old at the start of the study. The female was born in 1978, and was 13 years old when the study commenced. Male #5 was born 16 June 1991, at the start of the study. A second pup (not used in the study) was born to this female on 24 June 1992 and was released onto Sable Island when weaned. The female aborted a fetus 27 March 1993 and was not pregnant in 1993-94. The three youngest seals were born at the facility (to the female) and the three oldest were introduced into captivity as pups.

Animals were kept in an outdoor compound year-round at the Ocean Sciences Centre (Logy Bay, Newfoundland), and allowed to associate freely. Their enclosure consisted of 3 tanks (80, 5, and 4.5 m^3) containing ambient sea water, surrounded by $100m^2$ of wooden decking for hauling out (Figure 1). Animals were fed previously frozen herring (*Clupea harengus*) *ad libitum* for 30 min, once per day (see Chapter 5).

General Methodology:

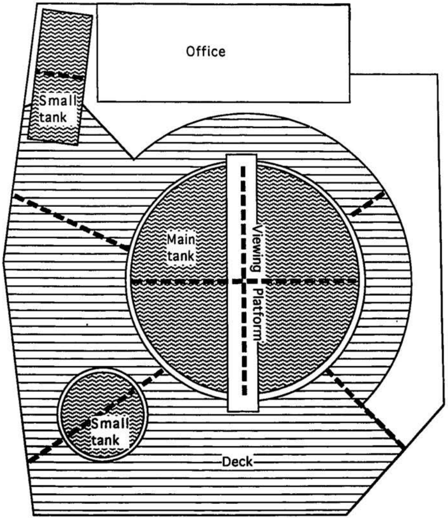
As most of the data collection methods are consistent across different aspects of the study, they are discussed collectively here. Additional details, specific to different analyses, are presented in the appropriate chapters.

Changes in several variables are described in reference to the day of the year (DOY). This is a cumulative measure commencing 01 January (Day 01) and ending 31 December (Day 365 or 366, when appropriate).

A set of morphological measurements was taken once a week, with data collection for

Figure 1:

Schematic of the harbour seal holding compound. The thick dotted lines represent the sectioning of the deck, main tank, and two smaller tanks for activity scores (Chapter 9).


Office
Small tank
Main tank
Viewing Platform
Small tank
Deck

the present study commencing in June 1991 and ending in December 1993. Each week, and prior to each metabolic determination (Chapter 7), the seals were weighed on a hanging platform attached to a scale. Mass was measured with an analog scale (accurate to 500 g) until 20 October 1991 and, thereafter, with a digital scale (accurate to 200 g). The seals were trained to hold position on the scale until a stable reading was achieved.

A series of girth and blubber depth measurements were also taken weekly. Girths were measured with a 2 m plastic tape measure at six sites along the body (Figure 2), according to the divisions suggested by Gales & Burton (1987). Measurements of blubber depth were taken dorsally at these same six sites (labeled #1 through #6, from anterior to posterior). Lateral blubber depths were also measured at these sites, with the exception of site #1 (the head). Measures of girth and blubber depth were taken while the seal was ventrally recumbent; as the animals were neither physically nor chemically restrained, it was not possible to obtain ventral blubber depth estimates. Blubber depth estimates were obtained using a portable ultrasonic depth probe (Ithaco Scanoprobe, #731A) which was calibrated against a Plexiglas rod supplied for that purpose. To enhance the consistency and clarity of blubber depth readings, mineral oil was used as a contact substrate and the six dorsal sites were shaved just after the moult.

Four additional categories of data were collected over the course of the study, although logistical and equipment constraints prevented these data from being collected over the entire study period (Figure 3). Fecal samples were collected on an opportunistic basis from 17 June 1991 to 27 April 1993, in order to estimate fecal energy loss (Chapter 6). Estimates of metabolism were obtained using indirect (gas) calorimetry, from 14 July 1992 (after a series of acclimation trials) until 02 November 1993 (Chapter 7). Also, between 22 April 1991 and 25 May 1992 rectal temperatures were measured to 0.1°C with a digital thermometer and thermal probe (Chapter 8). Finally, activity scores within the compound were obtained from 15 June 1991 to 15 July 1992 (Chapter 9).

Figure 2:

Sites for weekly morphological measurements, as *per* Gales & Burton (1987). Abbreviations are as follows: G = girth, D = dorsal blubber depth, and L = lateral blubber depth.

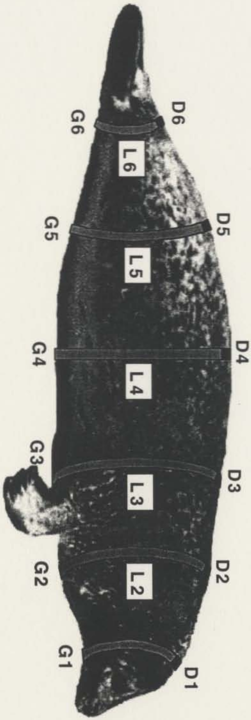
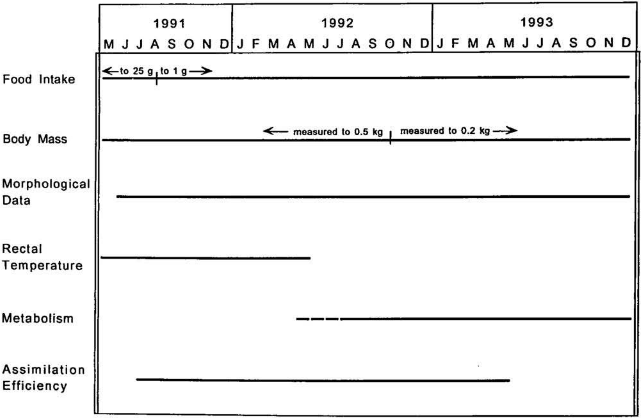

G1
G2
G3
G4
G5
G6
L2
L3
L4
L5
L6
D1
D2
D3
D4
D5
D6

Figure 3:

Schedule of data collection for the study. Also marked are changes in the accuracy for measuring food intake and body mass. The dotted line for the metabolic data indicates preliminary, acclimation trials.


1991
1992
1993
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
Food Intake
to 25 g
to 1 g
Body Mass
measured to 0.5 kg
measured to 0.2 kg
Morphological Data
Rectal Temperature
Metabolism
Assimilation Efficiency

Bioenergetic Theory:

Bioenergetics may be defined as the study of the factors which affect the thermal balance in animals, and the ways in which the energy of the organic components of their diets are used to support growth and reproduction (Blaxter 1989). The scope of such an area of research is vast, ranging from the examination of events taking place at the molecular level to studies at the level of the population.

Renouf & Noseworthy's (1990; 1991) studies examined the statistical relationship between changes in food intake and body mass in captive harbour seals. Due to the nature of their data it was not possible to integrate these components and quantify their impact upon the seals' energy budgets. The present study quantified the energy available to other bioenergetic parameters from energy intake and changes in body mass and composition. It utilized a bioenergetic framework which afforded three advantages. First, it provided a common currency (energy) by which many of the components could be more directly compared to each other and to other studies. Second, it allowed for a standard nomenclature of well-defined components of the energy budget. Third, it provided a model within which to investigate the possible effects and interactions of these seasonal changes.

The study of bioenergetics is based upon the principles derived from the First Law of Thermodynamics. Thermodynamics deals with the energetic characteristics of systems, that is, regions which are separated from others by real or conceptual boundaries. The First Law of Thermodynamics proposes that the energy content of a system can be changed from an initial state, E_i, to a final state, E_f, by inputs of heat and work. This relationship can be summarized according to the equation:

$$E_f-E_i=\Delta E=q-w$$

where ΔE is the change in the internal energy of the system, q is the amount of heat absorbed by the system and w is the work done by the system.

The practical implications of this theory arise from the assumption that, given the indestructible nature of energy, it should be possible to fully account for the energy changes in a system, whether this be a population, ecosystem, or individual. Specifically, the energy entering a biological system can be accounted for by the summation of the energy leaving the system and changes in energetic state taking place within it. Most bioenergetic research takes place at the level of the individual and is usually concerned with the construction of an *energy budget* (which reflects *energy balance*). Energy budgets attempt to account for the utilization of the energy consumed in food, losses of energy by processes such as excretion, metabolism and thermoregulation, and energy retained or utilized by the body through its chemical components.

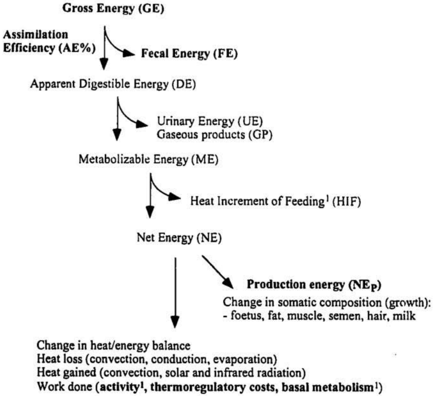
Energy budgets can become quite complex, and integration of studies focusing at different levels may be difficult. This problem is alleviated by the utilization of a common currency: energy. While some standardization of energetic measurements has been induced by the use of the SI units, variations still exist (appropriate conversions have been given in Appendix A). Unfortunately, a standard nomenclature has not evolved for the various components of the energy budget. The terms and divisions adopted in this study largely derive from those summarized by the National Research Council (1981) and Lavigne *et al.* (1982), with additional contributions from Blaxter (1989) (Figure 4).

One of the main components of the bioenergetic system in vertebrates is the input of energy from food which comprises the *gross energy intake* **(GE)** of the animal (also called *ingestion rate* in ecological studies). However, not all gross energy is available as usable energy, as a portion is lost through three main 'waste' products: *fecal energy loss* **(FE)**, *urinary energy loss* **(UE)**, and the *heat increment of feeding* **(HIF)**. The energy available after the removal of FE, UE, and HIF from GE is termed *net energy* **(NE)**, and is the energy that is actually available to the animal for maintenance, growth, and work, such that:

$$NE = GE - (FE + UE + HIF).$$

Figure 4:

Schematic representation of bioenergetic terms used in this study. The conventions are a combination of those proposed by the National Research Council (1981), Lavigne *et al.* (1982) and Blaxter (1989). Components calculated in this study are marked in bold. Note that HIF was not measured directly, but was estimated for ringed and harp seals, and rectal temperatures were measured as an indication of thermoregulatory costs.



[1] Expended as heat and may contribute to 'heat gained'.

Fecal energy (also: *egesta rate* or *defecation rate*) is primarily comprised of energy lost to the system through undigested food. However, secretions into, and cellular debris from, the gastro-intestinal tract, as well as enteric microbes and their products also contribute to FE. The removal of FE from GE leaves the *apparent digestible energy* **(DE)**, the energy which passes through the gut wall and into the blood stream of the animal. It is often measured in terms of digestive or *assimilation efficiency* **(AE%)** such that:

$$AE\% = DE/GE \times 100.$$

Energy is also lost through the production and excretion of urine (UE). This loss is a necessary end process of protein catabolism, removing nitrogenous end products such as urea, creatine, etc. *Metabolizable energy* **(ME)** is defined as the energy remaining after the removal of FE, UE and the gaseous products of digestion (e.g. methane, hydrogen) from GE.

While FE and UE represent physical waste products that can be collected and measured, the heat increment of feeding (HIF, Harris 1966; also: Specific Dynamic Action, Beamish *et al.* 1975; Kleiber 1975; Specific Dynamic Effect, Rubner 1902; Heat of Nutrient Metabolism, Moen 1968; Diet-induced Thermogenesis, Rothwell & Stock 1979) represents the increase in metabolism during feeding and digestion. The biochemical processes resulting in this increased heat production are not well understood (Mitchell 1962; Blaxter 1989), although it is thought to partially result from the breakdown of complex organic compounds, such as the deamination of amino acids in the liver (Buttery & Annison 1973). The amount of HIF is at least partly dictated by the size and composition of the diet (Hoch 1971). The energetic cost of processing food is lowest for lipids (16% of GE) and highest for protein (32% of GE) and carbohydrates (Blaxter 1989). Unfortunately, studies have shown that HIF can not be calculated directly from a knowledge of diet composition, as mixed composition foods result in a lower than predicted HIF (Nair *et al.* 1983). It has also been suggested that, at least in marine vertebrates, HIF may partially be the result of raising prey items to body temperature (Wilson & Culik 1991).

The role of HIF in a bioenergetic system is ambiguous, as it does not always represent an energetic loss *per se*. Although usually referred to as a 'waste product', HIF can be useful when retained by animals below their thermoneutral zone to stave off hypothermy, thereby reducing the energy needed to maintain homeothermy (Lavigne *et al.* 1982). However, the opposite is true if HIF exceeds thermal maintenance requirements and contributes to hyperthermy. The heat increment of feeding represents the energy lost between ME and NE and may be expressed as a proportion of metabolizable energy. Conversely, the proportion of ME that is retained in the body is defined as *the efficiency of utilization of metabolizable energy* (i.e., NE/ME x 100, or [HIF-ME]/ME x 100).

Net energy is proportional to GE (although not linear) such that, for every increase in GE there is an increase in NE, as well as an increase in the amount of energy released as heat. Net energy is the energy available to the animal for performing various functions. Lavigne *et al.* (1982) divided this into maintenance energy (**NE_m**) and production energy (**NE_p**). In their paper the former includes the costs of basal metabolism, activity, and thermoregulation while the latter includes work and energy storage in terms of growth. The present study differentiates between NE_P (which is defined soleiy as energy storage due to mass changes) and the cost of work.

Blaxter (1989) partitioned net energy into the components *heat production* and *heat retention*. Heat production comprises energy changes due to work, heat stored, and heat lost (via convection, conduction, evaporation). Retention refers to energy devoted to somatic growth, and is equivalent to NE_P in the present study. All bioenergetic schemes are complicated by the fact that work, activity, and metabolism not only consume energy but also generate heat. In addition, energy input from solar or infrared radiation will contribute to thermal balance.

The present study quantified the energetic contribution of food intake and changes in body mass upon the seals' energy budgets. This value represents the energy available to other parameters of the bioenergetic system, hereby defined as *available energy* **(EA)**. As increases in body mass constitute a positive NE$_P$ value, EA was calculated as the difference between GE and NE$_P$ (i.e., EA = GE - NE$_P$).

Chapter 3 - Seasonal Changes in Body Mass

Introduction:

Needham (1964) suggested that homeotherms and poikilotherms, with the exception of short-lived species, demonstrate seasonal changes in body mass, superimposed upon their primary growth patterns. Seasonal changes in body mass or body fat have been documented in numerous phocid species, including grey (Fedak & Anderson 1982; Fedak & Anderson 1987), ringed (Ryg *et al.* 1990; Ryg & Øritsland 1991), harp (Stewart & Lavigne 1984; Beck *et al.* 1993b; Renouf *et al.* 1993; Lager *et al.* 1994), hooded (Bowen *et al.* 1987; Kovacs & Lavigne 1991; Oftedal *et al.* 1993), elephant (Costa *et al.* 1986; Fedak *et al.* 1989; Slip *et al.* 1992; Boyd *et al.* 1993) and harbour seals (Boulva & McLaren 1979; Ashwell-Erickson & Elsner 1981; Pitcher 1986; Härkönen & Heide-Jørgensen 1990; Reilly & Fedak 1991).

Seasonal changes in body mass at least partially reflect changes in energy balance. In mammals, fat deposits are thought to have evolved to act primarily as a readily convertible energy reserve (Pond 1977; Pond & Ramsay 1992). Hence, seasonal mass changes in many high-latitude mammals are thought to reflect seasonal variability in nutrient availability (Holand 1992). Renouf & Noseworthy (1990; 1991), however, demonstrated that captive harbour seals exhibited significant changes in mass despite unrestricted access to food.

Among phocids, the period of greatest mass loss usually occurs during the breeding and moult seasons when reproductive and thermal costs (including lactation and activity) are highest, and food intake is restricted (Chapter 5). This association with reproductive costs led Bryden (1969) to hypothesize that seasonal changes in body mass should be greater in mature than immature seals, and greatest in breeding females (*cf.* Leader-Williams & Ricketts 1982). This chapter examines the extent and pattern of seasonal mass changes in the captive harbour seals. It also investigates possible effects of age and reproductive status, and compares the observed patterns to those reported for other pinniped species.

It is important to quantify the extent of seasonal changes in mass as a first step in determining their bioenergetic effect, as large changes in body mass can have a significant effect on a seal's energy budget. Seasonal deposition and utilization of body components directly contributes to available energy through production energy (Chapter 4). In addition, seasonal variation in body mass can affect metabolic rates, which are at least partially mass-specific (Chapter 7), and can also impact upon thermoregulatory costs (through changes in the insulative blubber layer; Chapter 8).

Finally, most energetic models incorporate only those changes in body mass associated with net annual growth. Given the aforementioned bioenergetic effects of changes in body mass, it is important to quantify and describe circannual variation for incorporation into such models.

Statistical Descriptions:

Circannual changes in body mass (M) were calculated as the maximum change (in kg) during a calendar year ($\Delta M = M_{max} - M_{min}$). Mass changes were also calculated as a percentage of maximum mass for that year (Percent change = $\Delta M/M_{max} \times 100$). Seasonal variation in body mass was divided into four periods, and mass changes within each period were calculated in terms of both absolute mass and as the ratio of mass change to mass at the start of that period (= $\Delta M/M_{init} \times 100$).

The pattern of seasonal mass changes was described by mathematical functions relating relative mass (calculated as the ratio of observed to mean annual mass) to day of the year (DOY) within each period. Mathematical descriptions were derived using data from the three oldest males (#1-3). These formulae were then applied to data from males #1-4, and for males #1-3 and the female. Data from all three study years were used in the derivation and testing of these formulae, except for the 1993 female data which was regarded as atypical due to the loss of a fetus in March.

Results:

The harbour seals showed substantial circannual variation in body mass (Table 1, Figure 5). For males #1-4, mass varied by 15-32 kg (21.9 ± 8.8 kg, mean ± SD) during the year, which represented an annual percent change of 16-30% (23.7 ± 4.7%). Annual percent mass changes were greatest for the female in the years she gave birth to a pup (48.6 and 41.4%), and was within the range of that exhibited by the four oldest males in the year she did not produce a pup (28.3%). Mass changes exhibited by the youngest male (#5) were a product of constant net annual growth, which declined progressively during the study (46.9%, 33.9% and 23.0% increases in 1991, 1992 and 1993, respectively). Only in 1993 (the last year of the study) did male #5 (then 2 yrs old) exhibit any indication of seasonal variation in body mass.

The seals exhibited two distinct cycles of mass loss and gain during the year (Table 2, Figure 6). These were labeled chronologically as periods of primary mass loss, primary mass gain, secondary mass loss, and secondary mass gain. As mentioned previously, the youngest male did not exhibit predictable seasonal variation in body mass in 1991 and 1992, and so the data from this individual were not included in any of the descriptions or statistics presented below. When describing mass changes, 'initial mass' refers to the mass of the seal at the start of that period.

The period of primary mass loss coincided with the start of the reproductive season (early June), 1-3 weeks prior to the birth of a pup. This loss continued for a 2-month period, until late July/early August, shortly after the pup was weaned. During this period the male seals lost 16-28% of their initial mass, while the female lost 49% (1991) and 41% (1992) (Table 3). This pattern was different for the female in 1993, the year she did not give

Table 1:

Changes in body mass (M) during the calendar year. The dates of the first occurrence of the minimum and maximum mass during the year are given. Mass changes are expressed in terms of absolute mass (kg; $\Delta M = M_{max} - M_{min}$) and as percent change ($= \Delta M/M_{max} \times 100$). Note that data for 1991 encompassed only June to December, inclusive.

Year: 1991 (partial)

Subject	Maximum		Minimum		Mass Change	Percent Change
	Mass (kg)	Date	Mass (kg)	Date		
Male 1	105.5	May 27	79.0	Aug. 26	26.5	25.1
Male 2	102.0	Jun. 10	70.0	Sep. 23	32.0	28.4
Female	107.0	May 27	55.0	Aug. 1	52.0	48.6
Male 3	97.0	Jun. 10	74.0	Aug. 19	23.0	23.7
Male 4	85.0	Jun. 25	68.0	Oct. 21	17.0	20.0
Male 5	32.0	Dec. 23	17.0	Sep. 30	15.0	46.9

Year: 1992

Subject	Maximum		Minimum		Mass Change	Percent Change
	Mass (kg)	Date	Mass (kg)	Date		
Male 1	109.0	Dec. 22	77.5	Aug. 4	31.5	28.9
Male 2	94.5	Jun. 8	68.0	Aug. 4	26.5	28.0
Female	107.5	Jun. 15	63.0	Aug. 4	44.5	41.4
Male 3	95.0	Jun. 2	80.0	Aug. 4	15.0	15.8
Male 4	88.5	Jun. 15	72.0	Aug. 11	16.5	18.6
Male 5	49.2	Dec. 15	32.5	Jan. 16	16.7	33.9

Table 1 (continued):

Year: 1993

	Maximum		Minimum		Mass	Percent
Subject	Mass (kg)	Date	Mass (kg)	Date	Change	Change
Male 1	110.0	Dec. 22	79.2	Aug. 30	30.8	28.0
Male 2	98.6	Jun. 7	75.0	Sep. 21	23.6	23.9
Female	91.2	Jan. 12	65.4	Aug. 30	25.8	28.3
Male 3	99.2	May 25	72.8	Aug. 9	26.4	26.6
Male 4	89.2	Jun. 23	73.8	Aug. 30	15.4	17.3
Male 5	62.6	Dec. 14	48.2	Jan. 26	14.4	23.0

Figure 5:

Weekly measures of body mass (kg). Data are presented for each of the six harbour seals separately for the 1991 (solid line, circles), 1992 (broken line, squares) and 1993 (dotted line, triangles) study years. Note the scale difference in the graph for male #5.

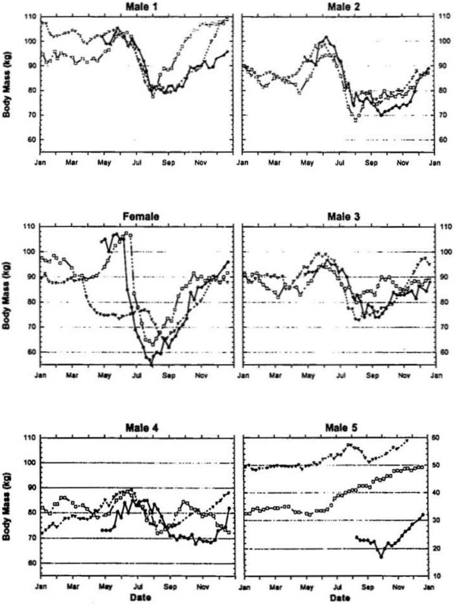

Male 1
Male 2
Female
Male 3
Male 4
Male 5
Body Mass (kg)
Body Mass (kg)
Body Mass (kg)
110
100
90
80
70
60
50
40
30
20
10
Jan
Mar
May
Jul
Sep
Nov
Jan
Date
Date

Table 2:

Changes in relative body mass (y) with day of the year (x). Relative body mass was calculated as the ratio of observed to mean annual mass. Relative mass calculations for 1991 utilized the mean mass from the 1992 data. The year has been partitioned into four phases, defined by day of the year (DOY). The formulae have been applied to three sets of data: males #1-3, males #1-4, and males #1-3 and the female. Data for the males are from all study years, while data for the female are from 1991 and 1992 only. The proportion of the variance explained (r^2) and its statistical significance is given for each of the data groups for each of the phases.

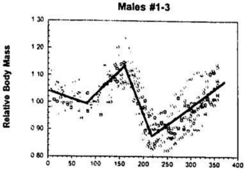
		Proportion of Variance Explained		
Phase DOY	Formula	Males 1-3	Males 1-4	Males 1-3 & Female
Phase 1				
Day 05-83	$y = 1.040 - 0.000488x$	.09*	.05*	.04
Phase 2				
Day 83-161	$y = 0.812 + 0.002012x$	.56**	.49**	.55**
Phase 3				
Day 161-217	$y = 1.994 - 0.005165x$	.74**	.59**	.72**
Phase 4				
Day 217-370 (05)	$y = 0.573 + 0.001353x$	.56**	.40**	.46**

* significant at $p \leq 0.05$

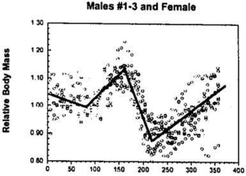
** significant at $p \leq 0.01$

Figure 6:

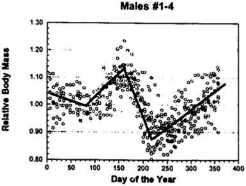
Changes in relative body mass with day of the year. The lines represent the four mathematical formulae given in Table 2. The data were pooled from all three study years, except for the female where only data from 1991 and 1992 were used. The three graphs represent three data sets: males #1-3 (top), males #1-3 and the female (middle), and males #1-4 (bottom). Relative body mass was calculated as the ratio of observed to mean annual body mass. Data from 1991 were compared to the mean annual mass from 1992.



Males #1-3



Males #1-3 and Female



Males #1-4

Table 3:

Changes in body mass by period. Mass changes during each period are expressed in terms of absolute mass (kg; $\Delta M = M_{max} - M_{min}$) and percent change, calculated as the ratio of absolute mass change to initial mass at the start of that period ($\Delta M/M_{init} \times 100$). Data are presented for each of the six study animals, for each of the four period of mass change, for each year.

Period of Primary Mass Loss - 1991

Subject	Begins	Ends	Mass change (kg)	Percent change
Male 1	late May	late Jul.	105.5-80.0	-24.2
Male 2	early Jun.	late Jul.	102.0-74.0	-27.5
Female	late May	late Jul.	107.0-55.0	-48.6
Male 3	early Jun.	mid Aug.	97.0-74.0	-23.7
Male 4	late Jul.	mid Sep.	85.0-69.5	-18.2
Male 5	mid Sep.	late Sep.	22.5-17.0	-24.4

Period of Primary Mass Loss - 1992

Subject	Begins	Ends	Mass change (kg)	Percent change
Male 1	mid Jun.	early Aug.	103.5-77.5	-25.1
Male 2	mid Jun.	early Aug.	94.5-68.0	-28.0
Female	mid Jun.	early Aug.	107.5-63.0	-41.4
Male 3	early Jun.	early Aug.	95.0-80.0	-15.8
Male 4	mid Jun.	early Aug.	88.5-72.0	-18.6
Male 5	n/a	n/a	34.0-41.0[1]	+20.6

Table 3 (continued):

Period of Primary Mass Loss - 1993

Subject	Begins	Ends	Mass change (kg)	Percent change
Male 1	late May	late Jul.	104.4-80.6	-22.8
Male 2	early Jun.	early Aug.	98.6-76.4	-22.5
Female[2]	late Mar.	early May	88.8-74.6	-16.0
Female	mid Jul.	end Aug.	76.8-65.4	-14.8
Male 3	early Jun.	early Aug.	99.0-72.8	-26.5
Male 4	mid Jun.	early Aug.	89.2-74.6	-16.4
Male 5	n/a	n/a	50.8-57.2[1]	+12.6

1. Male #5 did not show a corresponding period of mass loss, but mass changes are given for the equivalent periods, from mid Jun. to early Aug. 1992, and from early Jun. to early Aug. 1993.
2. The female underwent two distinct periods of mass loss. One may have been related to the loss of the fetus. The percent mass loss from the start of the first period to the end of the second (88.0-65.4 kg) was 26.4%.

Plateau and Primary Mass Gain - 1991

Subject	Plateau until:	Mass gain until:	Mass change (kg)	Percent change
Male 1	mid Sep.	late Dec.	80.0-96.0	+20.0
Male 2	mid Sep.	early Jan.	70.0-90.0	+28.6
Female	n/a	early Jan.	55.0-97.5	+77.3
Male 3	mid Sep.	early Jan.	74.0-91.0	+23.0
Male 4	mid Nov.	late Dec.	68.5-82.0	+19.7
Male 5	n/a	n/a	22.5-32.5[3]	+44.4

3. Male #5 data from mid-Sep. to early Jan.

Plateau and Primary Mass Gain - 1992

Subject	Plateau until:	Mass gain until:	Mass change (kg)	Percent change
Male 1	n/a	mid Dec.	77.5-109.0	+40.6
Male 2	n/a	early Jan.	68.0-89.8	+32.1
Female	n/a	late Dec.	63.0-91.6	+45.4
Male 3	n/a	early Jan.	80.0-91.6	+14.5
Male 4	n/a	late Sep.	72.0-84.5	+17.4
Male 5	n/a	mid Dec.	41.0-49.2	+20.0

Table 3 (continued):

Plateau and Primary Mass Gain - 1993

Subject	Plateau until:	Mass gain until:	Mass change (kg)	Percent change
Male 1	early Sep.	late Dec.	79.2-110.0	+38.9
Male 2	mid Sep.	mid Dec.	75.0-87.0	+16.0
Female	late Aug.	mid Dec.	74.8-97.4	+30.2
Male 3	late Aug.	mid Dec.	65.4-89.0	+36.1
Male 4	late Aug.	late Dec.	73.8-88.0	+19.2
Male 5	n/a	mid Dec.	52.6-62.6	+19.0

Period of Secondary Mass Loss - 1992

Subject	Begins	Ends	Mass change (kg)	Percent change
Male 1	late Jan.	mid Apr.	96.0-92.0	-04.2
Male 2	early Jan	mid Apr.	90.0-79.0	-12.2
Female	late Jan.	late Mar.	98.5-89.0	-09.6
Male 3	late Jan.	mid Apr.	91.5-83.0	-09.3
Male 4	mid Feb.	mid Apr.	86.0-78.0	-09.3
Male 5	n/a	n/a	34.5-33.0[4]	-04.3

4. Male #5 data from late Jan. until mid Apr.

Period of Secondary Mass Loss - 1993

Subject	Begins	Ends	Mass change (kg)	Percent change
Male 1	late Dec.	late Mar.	109.0-99.0	-09.2
Male 2	early Jan.	late Mar.	89.8-83.2	-07.3
Female	late Dec.	late Mar.	91.6-88.8	-03.1
Male 3	early Jan.	late Mar.	91.6-85.4	-06.8
Male 4	late Sep.	early Jan.	84.5-73.0	-13.6
Male 5	n/a	n/a	50.0-49.4[5]	-01.2

5. Male #5 data from early Jan. until late Mar.

Table 3 (continued):

Period of Secondary Mass Gain - 1992

Subject	Begins	Ends	Mass change (kg)	Percent change
Male 1	mid Apr.	early Jun.	92.0-103.5	+12.5
Male 2	mid Apr.	early Jun.	79.0-94.5	+07.0
Female	late Mar.	mid Jun.	89.0-107.5	+20.8
Male 3	mid Apr.	early Jun.	83.0-95.0	+14.5
Male 4	mid Apr.	mid Jun.	78.0-88.5	+13.5
Male 5	n/a	n/a	33.0-33.5[6]	+01.5

[6] Male #5 data from mid Apr. until early Jun.

Period of Secondary Mass Gain - 1993

	Begins	Ends	Mass change (kg)	Percent change
Male 1	late Mar.	mid May	99.0-104.4	+05.5
Male 2	late Mar.	mid May	83.2-98.2	+18.0
Female	n/a	n/a	-	-
Male 3	late Mar.	late May	85.2-99.2	+16.4
Male 4	late Jan.	early Mar.	73.0-78.6	+07.7
Male 4[7]	late Mar.	mid Jun.	77.2-89.2	+15.5
Male 5	late Apr.	late Jul.	48.2-57.4	+19.1

[7] Male #4 exhibited an extended period of mass gain. When combined, the overall mass change from late Jan. to mid Jun. (73.0-89.2 kg) was 22.2%

birth. For that year she exhibited an extended period of mass loss, commencing earlier (late March) and ending slightly later (late August) than in previous years. The percent mass change over this extended period was lower than in previous years (26%), due to a lower initial mass in late March, as her mass at the end of this period was almost identical to that in previous years. The pattern for the males did not change significantly whether or not the female produced a pup. The period of primary mass loss was sometimes followed by a shorter period (2-6 weeks) of constant body mass. This effect was absent in all seals during 1992, and the female in 1991.

The subsequent period was identified as one of primary mass gain. This usually commenced in September, towards the end of the moult, and continued until late December/early January. During this period the male seals increased their mass by 20-29%. The female increased her mass by 77% and 45% in 1991 and 1992, but only by 30% in 1993, the year she did not produce a pup. During the period of primary mass gain the seals recovered an average of 95.3 ± .07% of the mass they had lost during the previous period. There was a strong relationship between the percent body mass change during the periods of primary mass gain and primary mass loss. When data from all the seals (except male #5) for the three years were combined, the resulting correlation accounted for 80% of the observed variance ($F_{1,13}=54.7$, $p<.0001$, $r=.91$). This relationship was weaker when data from the female were removed to eliminate the statistical effect of non-continuous data ($F_{1,10}=9.4$, $p=.01$, $r=.70$).

Following these two periods of primary mass change, another cycle of less pronounced mass loss and gain was observed. The period of secondary mass loss occurred from early January until late March/early April. During this period the seals generally lost no more than 10% of their initial mass. In the following period of secondary mass gain, which lasted until the next period of primary mass loss, the seals gained back slightly more of their mass (105.3 ± 4.3%) than they had lost during the previous period.

Discussion:

The extent of changes in body mass due to reproductive costs are usually related to the intensity, synchronicity and duration of the breeding period (Loudon & Racey 1987; Horton & Rowsemitt 1992). These factors are a reflection of the type of mating system, which is at least partially determined by the seasonality and predictability of environmental conditions (Bartholomew 1970).

In many mammals a distinct period of mass gain occurs prior to the start of the mating period, as evidenced by the seals in this study. While this increase may partially compensate for the mass lost during the previous winter, its primary function is to prepare the animal for the energetic demands of the reproductive season (Young 1976; Pond 1978). These costs may include both inter- and intrasexual competition, lactation, decreased energy intake, and the provisioning and guarding of offspring and mates. In males, the pre-mating acquisition of body mass has been called the "fatted male" phenomenon (DuMond & Hutchison 1967) and is assumed to function as a secondary sexual characteristic. In male harbour seals, where reproductive effort is based solely upon intrasexual competition, this attribute also occurs. It is of particular interest that this increase in mass occurred among a group of captive harbour seals, where some of the costs of reproduction experienced by their wild counterparts (e.g., decreased feeding opportunities) were mitigated. Schusterman & Gentry (1971) observed that captive male California sea lions showed this seasonal increase in mass in synchrony with their wild counterparts, even when deprived of direct contact with females.

The period of primary mass loss exhibited by the seals in this study was closely tied to the start of the breeding season for both the males and the female. The high mass loss of the female in 1991 and 1992 was partially the direct result of the loss of the fetus at parturition, as well as the increased energy expenditure associated with lactation (Fedak & Anderson 1982; Costa *et al.* 1986; Oftedal *et al.* 1987; Fedak *et al.* 1989). The extended period of mass loss exhibited by the female in 1993 was probably related to the fact that she did not produce a pup that year. It is possible that the loss of the fetus in late March precluded the additional mass gain normally attained in the late spring (through additional blubber stores and growth of the fetus) and caused the early, extended period of mass loss.

In the years she nursed a pup, the female lost 41-49% of her initial mass during the breeding season, values which included the loss of the pup's mass. Removing this effect, the female lost 29% and 38% of her initial postpartum mass during the 1991 and 1992 breeding seasons, respectively. Bowen *et al*. (1992) reported that harbour seal females lost 33% of their initial postpartum mass (at a rate of 1.6 kg/d) during the first 80% (19 of 24 d) of the lactation period. They also suggested that increased foraging effort decreased the rate of mass loss towards the end of lactation, particularly for smaller females. In comparison, other phocid females have been reported to lose between 16-46% of their initial mass during the course of lactation (Table 4). Variation in these values is at least partially attributable to maternal size, the extent of feeding during lactation, and the length of the lactation period.

For the mature males, the period of mass loss extended over the entire breeding season, during which they lost from 16-28% of their initial mass. Many studies have noted the high reproductive effort of male harbour seals. In the wild, breeding male harbour seals spend two-thirds or more of their time in the water and are active in aquatic display behaviour and agonistic encounters with other males (Sullivan 1981; 1982; Thompson 1988; Thompson *et al.* 1989; Perry 1993; Walker & Bowen 1993b). The effects of such activity on body condition have been noted previously. Pitcher (1986) reported that male harbour seals lost body mass and exhibited reduced blubber thickness during the breeding season. More specifically, Härkönen & Heide-Jørgensen (1990) reported an 11-14% decrease in adult male mass during this period. Reilly & Fedak (1991), in a longitudinal study, found that the mean daily mass loss of males during the mating season was 1.0 kg/d.

Walker & Bowen (1993a), noting confusion in the literature, arbitrarily divided the

Table 4:

Relative mass loss during lactation among female phocids.

Changes in body mass calculated as a percentage of initial, post-partum mass.

Species	Percent Mass Lost	Source
Hooded	16	Bowen *et al.* 1987
Harp	27	Stewart 1986; Kovacs *et al.* 1991
Ringed	31	Hammill *et al.* 1991
Northern elephant	31	Costa *et al.* 1986
Harbour	33	This study
Hawaiian monk	34	Kenyon & Rice 1959
Southern elephant	37	McCann *et al.* 1989
Grey	38	Fedak & Anderson 1982
Weddell	46	Tedman & Green 1987

breeding season into premating (no/few receptive females) and mating periods (when pups start to wean and females become available for copulation). They found that most (n=17) adult male harbour seals gained or maintained mass during the first part of the study, and lost mass during the later part, while 5 males lost mass throughout the study. They also noted that the rate of mass loss accelerated through the breeding period; the adult males lost 2% of their initial mass during the premating period, and 23% in the mating period. This translated into an average rate of mass loss of 0.9 kg/d. Given that receptive females are available for about 30 d on Sable Island, Walker & Bowen (1993a) estimated that mature male harbour seals would lose up to 30 kg or 20-30% of their initial body mass during the breeding period. The empirical results obtained in this study compare favourably to their estimate.

In comparison, male grey seals have been reported to lose 17% (Walker & Bowen 1993a, using data from Anderson & Fedak 1985) and 25% (Baker *et al.* 1994, using data from Fedak & Anderson 1987) of their initial mass during the breeding season. Similar uncertainty surrounds mature male Antarctic fur seals who have been reported to lose either 24 or 30% of their initial mass (Walker & Bowen 1993a and Baker *et al.* 1994, respectively, both interpreting data from Boyd & Duck 1991). Male northern elephant seals, noted for their extended breeding fasts, lose 36% of their initial mass (Deutsch *et al.* 1990).

Walker & Bowen (1993a) also noted that subadult males (arbitrarily defined as those <92.5 kg) did not exhibit the same pattern of mass loss as mature males, but rather gained or maintained mass throughout the study. They suggested that seasonal mass change was hormone-dependent (probably androgen), a hypothesis previously put forward by Schusterman & Gentry (1971) for California sea lions. This is also consistent with Bryden's (1969) hypothesis that seasonal changes in body mass should be closely tied to sexual maturity. However, seasonal mass loss has also been reported among juvenile northern fur seals during the breeding season fast (Baker *et al.* 1994). The rate of mass loss was greater in juveniles than in mature males defending breeding territories, partially due to higher mass-specific metabolic rates. In the present study, the 5 year old male (#4) exhibited distinct circannual variation in body mass, while male #5 also gave some indication of seasonal cycles at 2 years of age (1993).

There is general agreement that many male harbour seals are probably in negative energy balance during the mating season (Pitcher 1986; Reilly & Fedak 1991; Walker & Bowen 1993a). This period may extend for several weeks or months, encompassing both the mating and moult periods (Pitcher 1986; Thompson 1987). This negative energy balance is the product of increased activity (and possibly increased basal metabolism) and decreased energy input (see Chapter 5). Although the relative contributions of these factors is still unclear, Renouf & Noseworthy (1990; 1991) found that decreases in mass were not directly related to decreases in food energy intake. Given the link between mass loss and sexual maturity in both wild and captive populations, mass loss is likely due to reproductive behaviour and not to prey availability.

The stabilization of body mass at the end of the period of primary mass loss that was observed in some years coincided with the latter portion of the moulting period. Many pinniped species lose mass throughout the moult, when they spend the majority of their time hauled out of the water to reduce thermoregulatory costs (Finley 1979; Thompson & Rothery 1987; Hindell & Burton 1988; Slip *et al.* 1992; Watts 1992; Worthy *et al.* 1992). The seals in the present study were likely able to maintain mass by having the opportunity to feed without having to enter the water, although wild harbour seals probably do not fast completely, either (see Chapter 5). The postmoult increase in mass documented in this study is also common among seals, serving to replenish depleted energy and insulative stores before winter. The proximate mechanism seems to be a concurrent increase in energy intake (Chapter 5), possibly facilitated by other bioenergetic changes.

The secondary cycles of mass loss and gain, exhibited by the seals in this study during the winter and spring, were less dramatic than the mass changes seen during the breeding season, but they were energetically important. The period of secondary mass gain was likely in preparation for the reduced energy intake and increased activity costs associated with breeding. However, it is still unclear what changes occurred in the seals' energy budgets to facilitate this gain in energy stores. Similarly, it is unclear what shifts in the energy budget resulted in the negative energy balance during the winter months, when energy reserves were utilized and body mass decreased.

There is clear evidence of seasonal mass cycles among the captive harbour seals. It is apparent that the greatest changes in mass were associated with the reproductive season, although seasonal changes in mass were not restricted to sexually mature animals. The source of the changes in the seal's energy balance is not known. The following chapters investigate several energetic parameters that may explain some of this variation observed in body mass.

Summary:

- Male harbour seals exhibited seasonal variations in body mass of 16-30% (15-32 kg), despite unrestricted access to food;
- the female displayed circannual mass changes of 48 and 41% in the years she gave birth, and 28% in the year she did not;
- seasonal mass changes were not evident in the youngest male; and
- the breeding period was characterized by high rates of mass loss, while the period of greatest mass gain occurred during the post-moult months.

Chapter 4 - Mass/Energy Conversions

Introduction:

Seasonal changes in body mass can affect energy budgets through thermoregulatory costs, basal metabolism, or the direct contribution of tissue formation and utilization. This chapter examines the effect of changes in body mass upon available energy (EA), through changes in production energy (NE_P). Production energy can be negative or positive, depending on whether mass is gained or lost, respectively. To properly evaluate this factor it was necessary to quantify the proportion of mass changes deriving from specific body components, as the blubber layer and the core tissues (the carcass and viscera) have significantly different energy densities.

Phocid seals possess a thick layer of hypodermal adipose tissue, which accounts for almost all of the animal's dissectable body fat (Bryden 1968). One of the primary functions of this layer is to provide a readily convertible energy source (Pond *et al.* 1992; Pond & Ramsay 1992). It would seem logical, therefore, that changes in body mass related to periods of high energy conservation and utilization would consist entirely of changes within this energy reserve. However, there are four reasons why this does not necessarily occur.

First, the external blubber layer serves to adjust buoyancy, streamline the body, and maintain thermoregulation. These functions, primarily thermoregulation, are often at odds with the depletion or build up of the blubber layer as an energy reserve. For example, although seals are able to augment or restrict the insulative value of the blubber layer through vasoconstriction or vasodilation (Irving 1969; Tarasoff & Fisher 1970; Irving 1973; Molyneux & Bryden 1975), there are still functional thermal limits to this layer. It has been suggested that the distribution and extent of the blubber layer represents a balance between these competing functions, at least partially determined by the seals' physical environment (and the degree to which insulation is a priority; Stewart & Lavigne 1980;

Worthy & Lavigne 1983a; Øritsland *et al.* 1985).

Second, the insulative effectiveness of the blubber layer is not solely a function of its depth. Ryg *et al.* (1988) and later Hokkanen (1990) noted that heat loss from a cylindrical body (such as a phocid morph) depends not upon the thickness of the blubber layer, but upon the ratio between blubber depth and the radius of the body (see Watts *et al.* 1993). From a morphological perspective this implies that, as the external blubber layer is depleted, the core tissues should also be reduced in order to maintain a constant insulative property (see Chapter 10).

Third, gross energy requirements may be fulfilled through utilization of lipid reserves, but other biochemical demands may not be. For example, all vertebrates require protein catabolism in order to provide amino acids and nutrients to the brain (Newsholme & Start 1973; Willis 1982). As the blubber layer contains very little protein, it must be garnered from the core tissues instead (particularly when no external source exists).

Fourth, not all growth is seasonal. In immature seals, mass change analyses are complicated by net annual growth, while mass changes in pregnant seals are affected by fetal growth and the birth of the pup.

Determining the compartmental source of changes in body mass necessitates being able to estimate the proportion of the body mass composed of the blubber layer, core musculature, and viscera, and how these change over time. In most energetic studies the core and viscera are combined, so that the main task is to differentiate between 'blubber' and 'core' tissues. There are several methods of determining changes in energy density and body composition. Seals may be cross-sectionally sampled and dissected, weighing the component parts to provide information on compartmental body composition. The components may be subsequently analyzed by bomb calorimetry and/or proximate composition analysis to provide estimates of energy densities.

Injected isotope markers (e.g., deuterium oxide and tritiated water) can be used to determine total body water content (e.g., Reilly & Fedak 1990; Boyd & Duck 1991; Lager *et al.* 1994). This method estimates compartmental volumes through assumed water content values for muscle and blubber. Apart from the methodological problems which may contribute to errors in measurement (Vaughan & Boling 1961; Nagy & Costa 1980; Costa 1987; Oftedal & Iverson 1987), the use of radio-isotopes is intrusive and is often restricted by cost considerations, and logistical and legal constraints.

Cross sections of the animal at specific intervals along the axis can be used to interpolate total blubber volume. Cross sections can be obtained by dissection or by x-ray or CT scanner technology (Markussen *et al.* 1992b).

Finally, anatomical measurements can be used in conjunction with a mathematical model to estimate the volume of the external blubber layer. This method has the advantage of being able to detect longitudinal differences and being non-invasive. The current study applied longitudinal girth and ultrasonic blubber depth measurements to a mathematical model which estimated the total volume of the blubber layer. This provided estimates of the proportion of the observed changes in total body mass that could be attributed to core and blubber components. These could then be used to estimate the effect of observed mass changes on the seals' energy budgets via changes in production and available energy.

Method:

As part of the weekly series of morphological measurements, estimates of blubber depth and girth were taken from 16 September 1991 until 30 December 1993 (Chapter 2). These measures were used to estimate the volume of the blubber layer, using a derivation of Gales & Burton's (1987) truncated cone model, modified for the absence of ventral fat depth measurements (Appendix B). Blubber depth was calculated as the average of dorsal and lateral blubber estimates, except for the most anterior reading where only a dorsal measure was obtained. In this method the seal was mathematically divided into five sections, discounting the portions anterior to the pinnae and posterior to the tail. The blubber volume for each section was calculated as the difference between two truncated cones, one representing total body volume, the other representing core tissue volume. Total blubber mass was calculated as the sum of the five resulting blubber volumes multiplied by an estimated blubber density of 0.935 gm/cm^3 (Renouf *et al.* 1993). Core mass was the remainder of blubber mass minus total mass. The original mathematical model has been empirically tested on harp (Renouf *et al.* 1993), southern elephant (Slip 1992), and northern elephant seals (Worthy *et al.* 1992).

Blubber mass was measured weekly for each seal. To determine changes in relative body composition, the proportion of estimated blubber mass to total body mass was also calculated. To test whether total blubber mass or relative body composition changed significantly during the year, the data were subdivided into winter/spring (January 1 to June 31) and summer/fall (July 1 to December 31) periods. This partitioned the data set into periods of relatively 'good' (high body mass) and 'poor' (low body mass) condition. This is the same division used to test for overall seasonal differences in other morphological data (Chapter 10). Only blubber mass data from 1992 and 1993 were used to avoid potential seasonal bias. Data from both years were pooled and unpaired t-tests were performed to test for significant differences for each seal. Results were considered significant at alpha ≤ 0.01.

For each seal, a least-squares linear regression was fitted between the calculated blubber mass and body mass (1991-93 data). The slope of the line (Mass = a + b[Blubber mass]) was assumed to represent the proportion of total mass that resulted from changes in the blubber layer. There was concern that this relationship might differ according to the seal's energy balance, so the data were subdivided according to whether the animal gained or lost weight during the week, and individual regression lines were determined for periods of mass gain and loss. Separate equations for mass to production energy conversions (one for each direction) were derived for each seal. These were dependent upon the proportion of total mass change attributable to the blubber layer, as derived from the regression analysis, and utilizing the energy densities and formulae given in Appendix C. Gains and losses in core tissues and blubber were converted to positive or negative values of production energy, respectively. The effect of changes in body mass on production energy was computed on a weekly basis (as this was the frequency of the morphometric measurements), and expressed as MJ/week.

As a way of estimating the margin of error inherent in the calculations, NE_P was also calculated making the assumption that all of the mass changes were derived from changes in the blubber layer. This is clearly false for the pregnant female and the growing juveniles, and runs contrary to most other studies of mass loss in pinnipeds. However, it does provide a maximum energetic value from mass loss and gain with which to compare our results from mixed composition mass changes.

Results:

There was a significant seasonal difference in the calculated total blubber mass during the year for all seals except male #5 (Table 5). There was also significant circannual variation in relative body composition. For the adult males, blubber mass accounted for 40-44% of total body mass in January, decreasing to only 21-23% in July/August. The values for minimum and maximum percent blubber were slightly higher for both the youngest male and the female.

For males #1, 2, and 3 the proportion of changes in body mass attributable to the blubber layer (as estimated by the slopes of the regression lines) was between 0.77-0.89, for periods of both mass gain and loss (Table 6). For male #4, the slope was also within this range (0.87) for the growth phase, but was lower for the period of mass loss (0.64). Data from the female yielded a slope of 0.78 during the period of mass loss and a slope of 0.91 during the period of mass gain. The youngest male (#5) displayed a slope of 1.50 during

Table 5:

Circannual variation in the external blubber layer, as estimated by truncated cone model. The mass of the blubber layer is expressed in both absolute terms (kg; top) and as a proportion of total body mass (bottom; blubber/body mass x 100). Mean ± 1 standard deviation are presented for each seal, with data divided into Winter/Spring (January 01 to June 30) and Summer/Fall (July 01 to December 31) periods, 1992 and 1993 data combined. Unpaired t-tests were used to detect seasonal differences. The range over the two years is also given.

Mass of Blubber Layer:

Subject	Winter/Spring	Summer/Fall	Range	T-test results
Male 1	35.49 ± 3.68	28.74 ± 7.79	17.8-43.4	$t_{82} = 4.7$, $p<.0001$
Male 2	27.91 ± 2.75	22.66 ± 3.89	15.5-33.9	$t_{82} = 6.7$, $p<.0001$
Female	33.59 ± 5.51	27.57 ± 6.83	17.0-43.9	$t_{82} = 4.6$, $p<.0001$
Male 3	29.27 ± 2.54	24.04 ± 4.57	16.8-36.4	$t_{82} = 6.4$, $p<.0001$
Male 4	24.64 ± 3.20	21.19 ± 3.10	15.6-32.1	$t_{81} = 4.9$, $p<.0001$
Male 5	16.18 ± 2.89	16.97 ± 2.26	11.1-21.7	$t_{80} = 0.9$, $p=.17$

Proportion of Body Mass:

Subject	Winter/Spring	Summer/Fall	Range	T-test results
Male 1	35.68 ± 2.57	30.27 ± 4.89	22.5-41.1	$t_{82} = 3.9$, $p<.0001$
Male 2	31.49 ± 2.53	28.28 ± 3.60	22.8-36.5	$t_{82} = 4.7$, $p<.0001$
Female	38.30 ± 3.50	34.55 ± 5.03	26.3-52.5	$t_{82} = 4.5$, $p<.0001$
Male 3	32.37 ± 2.89	28.22 ± 3.74	22.0-40.6	$t_{82} = 6.8$, $p<.0001$
Male 4	30.13 ± 3.26	26.85 ± 3.05	21.1-37.3	$t_{81} = 4.7$, $p<.0001$
Male 5	37.44 ± 2.06	34.46 ± 3.69	27.2-42.7	$t_{80} = 0.8$, $p=.26$

Table 6:

The proportion of body mass changes resulting from changes in the blubber layer. The values are estimated from the slope of the regression line:

Body Mass = a + b[blubber mass].

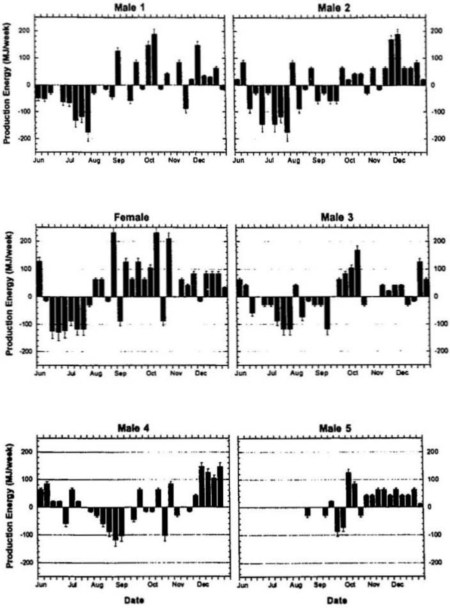
Data from each seal have been divided into weeks of mass loss and gain. Also listed are estimates of NEp due to these changes in body mass. Details of the derivation of compositional changes and energy values are given in Appendix C.

	Mass Increase		Mass Decrease	
Subject	%Blubber	NEp (kJ/g)	%Blubber	NEp (kJ/g)
Male 1	0.891	42.034	0.806	-29.183
Male 2	0.882	41.709	0.776	-28.307
Female	0.906	42.588	0.783	-28.511
Male 3	0.765	37.424	0.785	-28.570
Male 4	0.865	41.086	0.640	-24.334
Male 5	0.458	26.182	1.500	-47.570

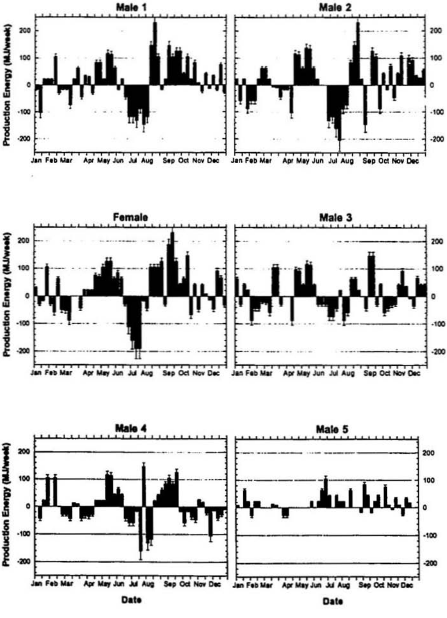
Figures 7a, b, c:

Production energy (MJ/week) calculated from weekly changes in body mass and composition. Data are presented separately for each of the six seals from 1991, 1992 and 1993. A positive production energy value indicates mass gain, a negative value indicates mass loss. Error bars are presented for estimates where 100% of the mass changes derived from changes in the blubber layer.

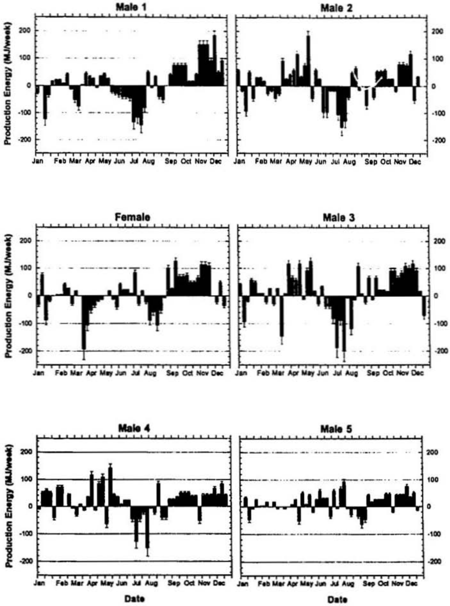
1991


Male 1
Male 2
Female
Male 3
Male 4
Male 5
Production Energy (MJ/week)
200
100
0
-100
-200
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Date

1992


Male 1
Male 2
Female
Male 3
Male 4
Male 5
Production Energy (MJ/week)
200
100
0
-100
-200
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Date

1993


Male 1
Male 2
Female
Male 3
Male 4
Male 5
Production Energy (MJ/week)
200
100
0
-100
-200
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Date

the period of mass loss and a slope of 0.46 during the period of mass gain.

Given the proportion of body mass change attributable to either the blubber layer or the core tissues, it was possible to estimate energy/mass conversion factors. The NE_P from the gain or loss of 1 g of body mass averaged 40.69 kJ and -27.60 kJ, respectively, for the four oldest males. The energy yield from 1 g of body mass for the female (NE_P = -28.51 kJ) was similar to the males, but the NE_P needed to gain 1 g of body mass was slightly higher (42.59 kJ). Male #5 had the highest energy yield from mass loss (47.57 kJ/g) and the lowest cost of mass gain (26.18 kJ/g). In comparison, Markussen *et al.* (1990) estimated the energetic value of changes in body mass for harbour seals at either 31.40 kJ/g (empirical results) or 33.50 kJ/g (derived from data in Webster 1983).

These data suggest that over 90% of the energy contributed to EA by NE_P was derived from the blubber layer. As the energetic contribution that mass changes made to the seals' overall energy budgets (via changes in EA) was directly proportional to the changes in body mass, the greatest effect was during the breeding season. In the mature seals, decreases in body mass contributed up to 200 MJ/week to EA. In the fall, during the period of primary mass gain, up to 200 MJ/week was diverted to tissue formation (Figures 7a, b, c).

Discussion:

It has often been assumed that seals will preferentially lose blubber over muscle mass, as the energy density of the former is greater. The extent of energy reserves among phocid seals is quite high, even compared to other northern mammals (Pond *et al.* 1992; Pond & Ramsay 1992). In this study, blubber mass in the adult males accounted for 40-44% of total body mass in the winter, decreasing to only 21-23% during the breeding season. Pitcher (1986) reported an average percent blubber of 27% for harbour seal males and 30% for females, while St. Aubin *et al.* (1978) gave an average value of 34-39%. In comparison, the proportion of total mass composed of lipids at the start of the breeding season was 39% for female northern elephant seals (Costa *et al.* 1986), 30-40% for female grey seals (Fedak & Anderson 1982; Reilly & Fedak 1990), and 45-50% for harp seals (Stewart & Lavigne 1984; Lager *et al.* 1994).

Despite the extent of the blubber layer, not all seasonal changes in body mass were derived from changes in this component. Under certain conditions thermoregulatory considerations may dictate that core mass is preferentially lost over blubber (Stewart & Lavigne 1980; Worthy & Lavigne 1983a; Øritsland *et al.* 1985; Beck *et al.* 1993b). This coincides with Ryg *et al.*'s (1988) hypothesis which predicts that, to minimize heat loss, seals should maintain a constant blubber wall thickness to body radius ratio. Therefore, once 'excess' insulation is lost, the animals should lose core mass, as well as blubber, to maintain a constant insulative value (see Chapter 10).

For the adult female, 78% of the mass lost over the entire year was accounted for by changes in the blubber layer. However, during the winter, the period of secondary mass loss (Chapter 3) was concurrent with fetal growth, inflating the yearly average. During the breeding season, only 70% of total body mass loss could be attributed to changes in the blubber layer. This compares favourably to the 69% reported by Bowen *et al.* (1992) from a cross-sectional study of nursing harbour seal females. Other studies have reported that 72%, 83%, 100%, and 100% of total mass loss derived from the blubber layer in nursing northern elephant (Costa *et al.* 1986), hooded (Bowen *et al.* 1987), harp (Stewart & Lavigne 1984, although see Chabot *et al.* 1995), and ringed seal females (Hammill *et al.* 1991), respectively.

For the adult males, an average of 25% of the total body mass loss was due to changes in core mass (lower in older animals, higher in younger ones). Markussen *et al.* (1992b) reported that approximately 40% of mass loss in male harbour seals was from the core tissue. However, these results were obtained using juvenile animals, on forced starvation, that had only a 30% starting percent blubber mass. In a previous account, Markussen *et al.*

(1990) estimated 70% of body loss was attributable to changes in the blubber layer. In comparison, male southern elephant seals lose 37% of their mass from core tissues during the moulting fast (26% from fat-free core tissues; Slip *et al.* 1992).

The slope derived for the youngest male (#5) during the growth phase (1.50) seems to suggest that, for every kg of body mass lost, there was a loss of more than 1 kg of blubber. However, the slope is a product of the core tissue growth which occurred even during the periods of overall mass loss so that, although he lost more than 1 kg of blubber, a partial offsetting amount of core mass was gained.

It should be noted that, unlike most other studies, the measures for the harbour seals were taken over an entire season. It is plausible that the proportion of core loss is higher during periods of greatest or most rapid mass loss, such as at the height of the breeding season. Although they did not investigate the source of the mass loss, Walker & Bowen (1993a) found that the rate of mass loss changed significantly in adult male harbour seals during different phases of the breeding season.

In contrast to the harbour seals in the present study, all of the seasonal mass changes exhibited by adult ringed seals (both male and female) reportedly derived solely from changes in the blubber layer (Ryg *et al.* 1990). Although there is a tendency for smaller phocid species to have proportionally more blubber (Ryg *et al.* 1993), they also accrue proportionally higher mass-specific metabolic demands (Kleiber 1975). The seasonal change in the ratio of blubber to total mass for the ringed seals was similar to that derived for the harbour seals, with females changing from 52 to 31% and males from 41 to 29% (Ryg *et al.* 1990). This suggests that ringed seals are probably not conserving core mass by being more heavily insulated than harbour seals.

Although relatively few subjects were used in the present study, mention should be made of the differences which were seen in the total blubber layer in reference to the gender and age of seals. In most high-latitude mammals the females usually possess greater fat reserves to offset the costs of lactation (Pond 1977; Pond 1978). In ringed seals (Ryg *et al.* 1990), mature females had a higher percent fat to body mass ratio, similar to that of the single female in this study. In contrast, Weddell seals display no such gender-specific difference (Bryden *et al.* 1984).

As discussed in Chapter 3, seasonal differences in growth will be overshadowed by primary growth patterns in younger seals, and less affected by the variation imposed by breeding costs. Therefore, in light of its energetic role, seasonal changes in the blubber layer should be more extensive in mature than immature seals. Ryg *et al.* (1990) reported more pronounced seasonal changes in body mass and blubber content in mature ringed seals, contrary to Smith (1987) who found no such age-related differences. Seasonal cycles in blubber content were more pronounced and distinct among the adults than the immature seal in this study, similar to results reported by Pitcher (1986).

While short-term changes in body mass may seem small, they make a significant contribution to an animal's annual energy budget. Failing to take the energetic impact of seasonal changes in body mass into account will seriously jeopardize the accuracy of bioenergetic estimates.

<u>Summary</u>:

- All except the youngest seal exhibited significant circannual changes in blubber mass and relative body composition;
- for the adult males, 64-89% of the observed changes in body mass were attributable to changes in the blubber layer; for the female these values were 78-90%; and
- production energy, resulting from changes in body mass, was estimated at ±200 MJ/week.

Chapter 5 - Changes in Gross Energy Intake

Introduction:

This chapter documents gross energy intake (GE) to determine the extent of circannual variation, and to compare the GE of the captive seals in this study to predictions made for other mammals. This chapter provides the data used in Chapter 6 to determine the effect of concurrent changes in GE and body mass on the seals' energy budgets.

Periods of fasting or curtailed food intake are a natural element of pinniped life history, and are often closely tied to reproductive strategy (Bonner 1984; Costa 1991). Seasonal changes in food intake have been documented in several captive pinniped species, including grey (Nordøy & Blix 1988; Kastelein *et al.* 1990b) and harp seals (Renouf *et al.* 1993; Lager *et al.* 1994), Steller (Kastelein *et al.* 1990a) and South American sea lions (Kastelein *et al.* 1995). The validity of some published estimates of energy intake is questionable, where animals have been kept in unnatural conditions (e.g., inappropriate thermal or photic regimes), or where food intake was quantified as ingested mass rather than energy (see Nordøy & Blix 1988; Kirkwood & Bennett 1992). The latter makes interpretation difficult, as changes in ingested mass may not accurately reflect changes in energy intake, particularly if the energy density of prey species changes significantly during the year. Additionally, different diets may vary greatly in energy density (e.g., between fish and invertebrate diets), making results across studies difficult to compare.

Previously, Renouf & Noseworthy (1990; 1991) documented seasonal changes in food intake in captive harbour seals. The present study examined energetic rather than food mass intake in order to make more direct comparisons with other studies and to integrate the data from several bioenergetic parameters. This study also examined changes in energy intake over an extended period, using animals with a wide range of ages. During the study some seals underwent periods of maximum growth, while some matured from juvenile to adult status. In addition, the female gave birth in two of the three study years.

Seasonal changes in GE can most easily be expressed as changes in total intake per time. However, given the large seasonal fluctuations in body mass, it is more physiologically appropriate to express energy intake in relation to body mass. A number of studies have investigated the allometric relationship between food intake and body mass for mammals in general (Kleiber 1961; Bourlière 1964; Kleiber 1975; Farlow 1976; Kirkwood 1983; Peters 1983) and marine mammals specifically (Sergeant 1969; Hinga 1979; Lavigne *et al.* 1982; Innes *et al.* 1986). Two of these will be used to compare the observed energy intake of the seals in this study with predictions derived from interspecific comparisons, and to document how these changed over the course of the year.

The empirical results will first be compared to the allometric relationship between energy intake and body mass among captive carnivorous mammals reported by Farlow (1976). Second, the data are compared to the allometric relationships relating energy intake and body mass for various groups of marine mammals derived by Innes *et al.* (1987). This latter study provides separate equations for mature or juvenile, growing or non-growing animals.

In addition, if energy intake is related to the metabolic requirements of body mass, it may be expedient to express GE as the ratio of energy to body mass$^{0.75}$. This equation is derived from Kleiber's (1975) allometric equation relating body mass to basal metabolic rate (see Chapter 7).

Focus on the ingestion rates of marine mammals has largely been driven by concerns for the effect these animals may have upon commercial prey species (e.g., Beddington *et al.* 1985). Documenting seasonal variation in energy ingestion rates is important for ecological modeling. Studies relating annual consumption rates to mean annual body mass will obscure patterns of seasonal change in prey consumption, particularly critical in migratory seal species which feed upon different stocks at different times of the year (such as harp seals in the NW Atlantic; Beck *et al.* 1993a; Stenson *et al.* 1995). In addition, many estimates of ingestion rates derive from short-term studies which have extrapolated their findings over an entire year. As discussed earlier, this will misrepresent true mean ingestion rates if the study period is not representative of annual intake. This problem is compounded by the limitation that many marine mammals are most accessible during their breeding and moulting periods when energy ingestion is likely to be most atypical of annual consumption rates (Stirling 1983; LeBoeuf 1986; 1991).

Method:

Seals were fed thawed herring (*Clupea harengus*) *ad libitum*, for 30 min, once per day. Seals were fed from individually marked buckets so that food mass intake (calculated as the difference between pre- and postfeeding fish mass) could be accurately determined. Fish mass was measured using either a hanging analog scale (10 kg x 25g until 7 August 1991) or a digital balance (5 kg x 1g, from 8 August 1991). The energy content of the consumed fish was estimated through proximate composition analysis of representative samples by Dr. F. Shahidi (Memorial University of Nfld.) and Dr. J. Lawson (Dept. of Fisheries and Oceans, St. John's).

Gross energy intake was summarized on both a weekly and monthly basis. Weekly GE is presented both as MJ/week and as a function of body mass. Although some studies calculate GE per unit body mass, this study uses the ratio: GE/body mass$^{0.75}$ (GE in MJ/week, body mass in kg), which is more closely related to metabolic expenditure (Kleiber 1975). A measure of relative monthly GE was calculated as the ratio of the mean daily GE for that month to the mean annual daily GE for that year. However, because the 1991 collection period commenced in June, the monthly data from that year were compared to the annual mean for 1992. While this provided a reasonable approximation for most seals, it did substantially bias the results for those seals (e.g., male #5) that exhibited large changes in GE between 1991 and 1992 due to growth.

A mixed-design (subject x year) ANOVA was used to test for differences in annual GE among seals in the 1992 and 1993 study years. As only partial data was available from 1991, a single factor within-subjects ANOVA was used to test for differences in total GE from June and December (inclusive) among all three study years. Annual changes in weekly GE were calculated as the absolute change (in kJ/week) during a calendar year ($\Delta GE = GE_{max} - GE_{min}$). Percent change in GE during the year was also calculated ($\Delta GE/GE_{max} \times 100$).

Observed monthly energy intake (expressed as kJ/d) was also compared to three predictions formulated by Innes *et al.* (1987). Their equation for non-growing, adult phocids ($GE=858.0M^{0.72}$; equation 8a, their paper, with GE converted to kJ/d and M in kg) was used to predict energy ingestion for the female and males #1 and #2. The formula for growing, adult phocids was applied to male #3 ($GE=534.82M^{0.80}$; equation 28). This formula was also applied to male #4 after June 1992. Prior to this, the equation for growing, juvenile phocids ($GE=2082.2M^{0.57}$; equation 30a) was applied. This last formula was also consistently applied to predictions for male #5. The observed levels of energy intake were also compared to the more general prediction made by Farlow (1976) for carnivorous mammals ($GE=915.84M^{0.697}$). Comparisons were made between predicted and observed values for each seal, on both a monthly and annual basis.

The pattern of seasonal changes in GE were described by mathematical functions relating relative GE (GE_r - calculated as the ratio of observed to mean weekly GE for that year) to day of the year (DOY) within each period. The mathematical descriptions were originally derived from data for the three oldest males (#1-3). These formulae were then applied to data from males #1-4, and for males #1-3 and the female.

Results:

The energy density of the herring (calculated as an average for each lot) ranged from 5.60-9.58 kJ/g (7.592 ± 1.371, mean ± SD) (Table 7). When energy density data were combined with food mass intake, there was no significant difference in total GE between June and December (inclusive) among the three test years (male #5 excluded from analysis; $F_{2,8}$=0.87, p=.45) (Table 8, Figure 8). Nor was there a significant difference in total annual GE between 1992 and 1993 ($F_{1,3}$=0.108, p=.98). Annual GE, averaged between 1992 and 1993, was 10865.7 MJ ± 871.5 for the four oldest males. Annual GE was significantly lower for the female (8321.5 MJ ± 880.8; $F_{\text{Scheffé}[2,3]}$=48.38, p=.045) and the youngest male (7590.3 MJ ± 1623.6; $F_{\text{Scheffé}[2,3]}$=65.50, p=.029).

The seals demonstrated substantial circannual variation in GE (Figure 9), with decreases during the year ranging from 50-90% (Table 9, Figures 10a, b, c). The female exhibited the greatest yearly variation in GE in any given year (range: 81-91%), regardless of whether she produced a pup or not.

When weekly GE was expressed as $MJ/kg^{0.75}$, it was apparent that the observed changes in GE were not merely a reflection of parallel changes in body mass. Although there were differences in the mean values for each seal, significant variation occurred throughout the year (Table 8, Figure 11). Mass-specific GE was lowest for the female in 1992 and 1993 (the two full study years) and, generally, highest for the two youngest males.

Description of cycles:

Changes in GE during the year could be described by four mathematical formulae relating GE_r to DOY (Table 10, Figure 12). The pattern of the changes was similar to those reported by Renouf & Noseworthy (1991) for food mass. The period of greatest decrease in GE commenced in early May, prior to the birth of the pup, reaching a minimum in late June, prior to weaning. However, GE increased quickly again to elevated levels in early

Table 7:

Composition and energy density of herring. Details of the proximate composition analyses for the various lots of herring used during the study, as identified by lot letter and last date fed (no overlap). Energy densities (kJ/g wet weight) were calculated from the composition data.

ID	Date end	%Lipid	%Protein	%Ash	%H_2O	Energy (kJ/g)
F	8-Aug-91	11.33	17.29	2.36	67.39	7.566
F1	18-Nov-91	7.58	18.75	2.10	71.42	6.354
H	31-Mar-92	13.88	16.65	2.17	66.99	8.454
I	1-May-92	9.92	17.35	3.54	69.19	7.023
J	8-May-92	6.31	17.39	2.31	73.99	5.610
K	21-May-92	6.35	17.26	2.70	73.69	5.603
M	4-Aug-92	15.38	15.52	2.56	66.54	8.841
N	10-Aug-92	9.31	16.12	1.97	72.60	6.561
O	31-Dec-92	12.62	16.57	2.83	67.98	7.944
P	1-Nov-93	12.74	17.82	2.43	65.39	8.216
Q	5-Nov-93	15.94	17.13	2.46	63.53	9.351
R	30-Dec-93	16.6	16.96	2.39	63.16	9.580
				Average ± S.D.		**7.592 ± 1.371**

Table 8:

Circannual variation in gross energy intake. Gross energy intake (GE) is expressed as an absolute (MJ/week; top) and mass-specific value (bottom). Mass-specific GE was calculated as the ratio of gross energy intake (MJ/week) to body mass ($kg^{0.75}$). Mean ± standard deviation are given for each subject for the three study years. Note that the values for 1991 are derived from data from June to December, inclusive.

Mean annual GE (MJ/week):

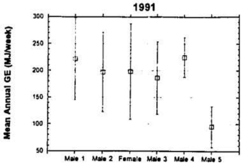
Subject	1991	1992	1993
Male 1	222.02 ± 79.64	209.81 ± 56.04	190.68 ± 58.62
Male 2	197.01 ± 74.22	197.76 ± 57.99	192.35 ± 43.31
Female	198.21 ± 89.39	170.56 ± 69.44	138.95 ± 51.73
Male 3	186.15 ± 67.61	195.02 ± 54.08	200.76 ± 47.04
Male 4	224.68 ± 37.17	203.91 ± 57.00	234.76 ± 42.56
Male 5	95.11 ± 38.11	123.68 ± 25.27	151.58 ± 30.72

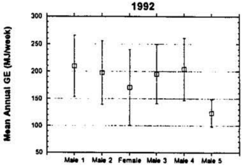
Mean annual mass-specific GE (MJ x $week^{-1}$ x $mass^{-0.75}$):

Subject	1991	1992	1993
Male 1	7.80 ± 3.12	6.77 ± 1.99	6.00 ± 2.07
Male 2	7.40 ± 3.12	7.14 ± 2.33	6.66 ± 1.65
Female	8.07 ± 3.92	6.22 ± 3.00	4.93 ± 1.92
Male 3	6.89 ± 2.69	6.68 ± 1.93	6.94 ± 1.76
Male 4	8.87 ± 1.73	7.53 ± 2.23	8.68 ± 1.73
Male 5	8.67 ± 3.49	7.96 ± 1.64	7.52 ± 1.55

Figure 8:

Mean annual weekly GE (MJ/week) for the six seals during the three study years. Note that the 1991 data are only from June-December, inclusive. Error bars are presented for 1 standard deviation.


1991
Mean Annual GE (MJ/week)
300
250
200
150
100
50
Male 1
Male 2
Female
Male 3
Male 4
Male 5


1992
Mean Annual GE (MJ/week)
300
250
200
150
100
50
Male 1
Male 2
Female
Male 3
Male 4
Male 5

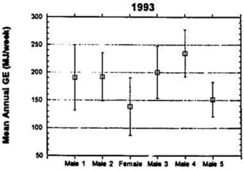

1993
Mean Annual GE (MJ/week)
300
250
200
150
100
50
Male 1
Male 2
Female
Male 3
Male 4
Male 5

Figure 9:

Estimates of weekly gross energy intake (MJ/week). Data are presented for each of the six harbour seals separately for the 1991 (solid line, circles), 1992 (broken line, squares) and 1993 (dotted line, triangles) study years.

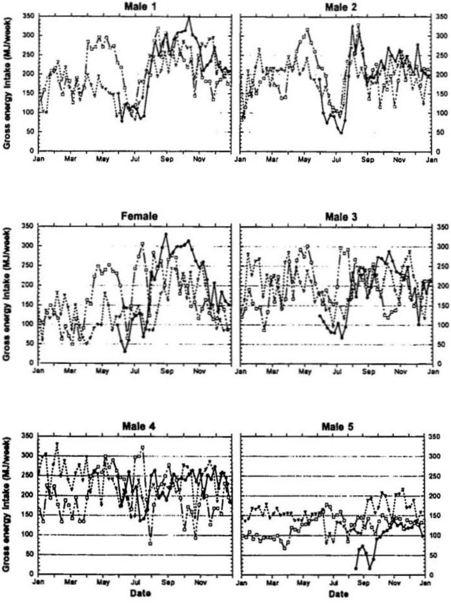

Male 1
Male 2
Female
Male 3
Male 4
Male 5
Gross energy intake (MJ/week)
0
50
100
150
200
250
300
350
Jan
Mar
May
Jul
Sep
Nov
Jan
Date

Table 9:

Changes in GE during the calendar year. Maximum and minimum values of weekly GE (MJ/week) are given for each year, as well as the date (start of the week) when they first occurred. Absolute change in energy (MJ) was calculated as the difference between the maximum and minimum values ($\Delta GE = GE_{max} - GE_{min}$). Percent change was calculated as a proportion of maximum GE ($\Delta G/G_{max} \times 100$). The maximum intake (and therefore estimates of annual change) may not be accurate for 1991 as peak consumption may have occurred prior to June (the start of data collection). The minimum for male #5 (1991) only reflects post-weaning weeks when he ingested measurable quantities of fish.

Year: 1991 (partial)

	Maximum GE		Minimum GE		Energy	Percent
Subject	MJ/week	Date	MJ/week	Date	Change	Change
Male 1	349.1	Oct. 13	77.4	Jun. 9	271.7	77.8
Male 2	326.4	Aug. 4	61.2	Jul. 7	265.2	81.3
Female	330.4	Sep. 1	30.8	Jun. 16	299.6	90.7
Male 3	288.5	Oct. 13	67.1	Jul. 14	221.4	76.7
Male 4	273.4	Dec. 1	136.0	Jul. 14	137.4	50.3
Male 5	136.7	Nov. 3	16.7	Sep. 15	120.0	87.7

Year: 1992

	Maximum GE		Minimum GE		Energy	Percent
Subject	MJ/week	Date	MJ/week	Date	Change	Change
Male 1	319.7	Aug. 16	103.8	Jun. 28	215.9	67.5
Male 2	329.2	Aug. 16	81.4	Jan. 5	247.8	75.3
Female	306.0	Jul. 19	49.2	Mar. 8	256.8	83.9
Male 3	301.2	May 10	86.4	Feb. 16	214.8	71.3
Male 4	322.6	Jul. 19	78.9	Aug. 2	243.7	75.5
Male 5	178.2	Jun. 21	67.8	Mar. 29	110.4	62.0

Table 9 (continued):

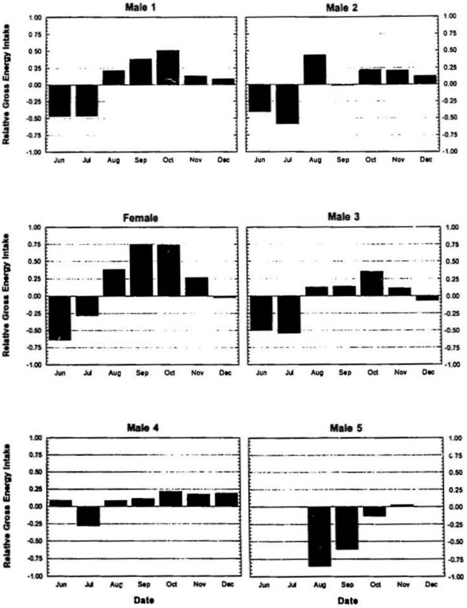
Year: 1993

Subject	Maximum GE		Minimum GE		Energy Change	Percent Change
	MJ/week	Date	MJ/week	Date		
Male 1	294.5	Nov. 28	82.1	Jul. 4	212.4	72.1
Male 2	265.4	Feb. 7	102.0	Jun. 27	163.4	61.6
Female	255.9	Nov. 7	49.1	Apr. 4	206.8	80.8
Male 3	287.4	Nov. 21	96.0	Jun. 27	191.4	66.6
Male 4	330.1	Feb. 7	144.8	Jun. 27	185.3	56.1
Male 5	217.0	Nov. 21	80.2	Jun. 20	136.8	63.0

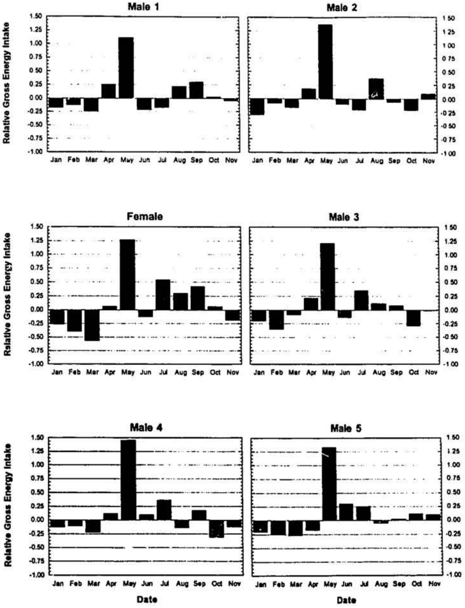
Figures 10a, b, c:

Relative monthly gross energy intake. Relative monthly GE was calculated as the ratio of mean daily GE (MJ/d) during that month to mean daily GE (MJ/d) during that year. Data are presented separately for the six seals during the three study years. Note that the 1992 data are presented on a different scale from 1991 and 1993.

1991


Male 1
Male 2
Female
Male 3
Male 4
Male 5
Relative Gross Energy Intake
1.00
0.75
0.50
0.25
0.00
-0.25
-0.50
-0.75
-1.00
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Date

1992


Male 1
Male 2
Female
Male 3
Male 4
Male 5
Relative Gross Energy Intake
1.50
1.25
1.00
0.75
0.50
0.25
0.00
-0.25
-0.50
-0.75
-1.00
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov
Date

1993

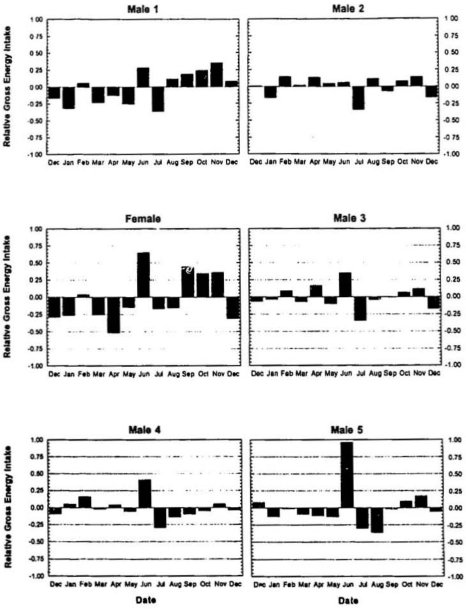

Male 1
Male 2
Female
Male 3
Male 4
Male 5
Relative Gross Energy Intake
1.00
0.75
0.50
0.25
0.00
-0.25
-0.50
-0.75
-1.00
Dec Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Date

Figure 11:

Estimates of weekly mass-specific gross energy intake. Mass-specific GE was calculated as the ratio of GE (MJ/week) to body mass ($kg^{0.75}$). Data are presented for each of the six harbour seals separately for the 1991 (solid line, circles), 1992 (broken line, squares) and 1993 (dotted line, triangles) study years.

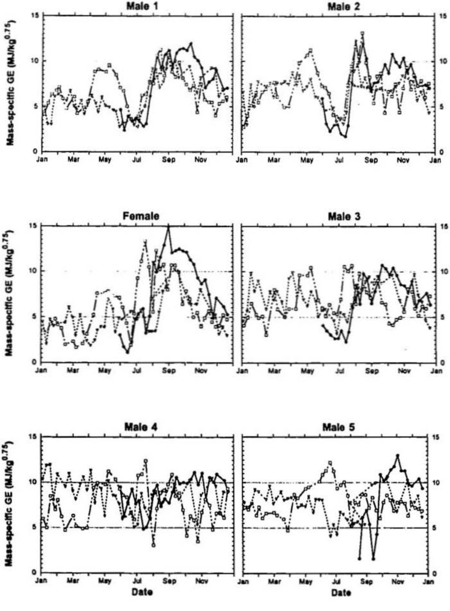

Male 1
Male 2
Female
Male 3
Male 4
Male 5
Mass-specific GE (MJ/kg$^{0.75}$)
0
5
10
15
Jan
Mar
May
Jul
Sep
Nov
Jan
Date

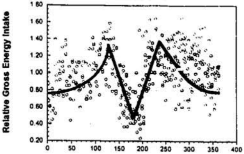
Table 10:

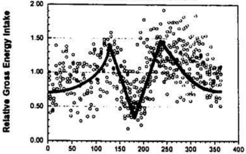
Changes in relative GE (y) with day of the year (x). Relative GE was calculated as the ratio of weekly gross energy intake to mean annual weekly GE. The year was partitioned into four phases, defined by day of the year (DOY). The formulae have been applied to three sets of data: males #1-3, males #1-4, and males #1-3 and the female. Data were pooled from all study years. The proportion of the variance explained (r^2) and its statistical significance is given for each of the data groups for each of the phases. All equations were significant at alpha ≤ 0.01.

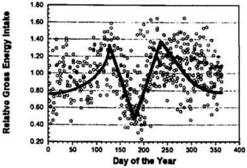
		Proportion of Variance Explained		
Phase DOY	Formula	Males 1-3	Males 1-4	Males 1-3 + Female
Phase 1 Day 12-124	$y = -2.0609 + 0.023247x$ $- 4.1909e\text{-}05x^2$	.38	.18	.28
Phase 2 Day 124-178	$y = 3.3287 - 0.016x$	.61	.49	.52
Phase 3 Day 178-237	$y = -2.2203 + 0.015164x$	.56	.36	.41
Phase 4 Day 237-377 (12)	$y = 1.0119 - 0.0044x$ $+ 5.0595e\text{-}05x^2$	.29	.14	.12

Figure 12:

Changes in relative weekly GE with day of the year. The lines represent the four mathematical equations given in Table 10. Relative weekly GE was calculated as the ratio of observed to mean annual weekly GE, with data from 1991 compared to the mean weekly GE from 1992. The data were pooled from all three study years. The three graphs represent three data sets: males #1-3 (top), males #1-3 and the female (middle), and males #1-4 (bottom).


Males #1-3


Males #1-3 and Female


Males #1-4

August, towards the middle of the moulting period. For some seals (particularly males #1 and #3) this level of increased energy intake was maintained for several weeks in 1991. For all seals, there was then a sharp decline in energy intake during the later moult period, followed by a more gradual decline in mid-January. There was then another increase in GE which reached a peak in mid-May. In some years, a 2-3 week period of depressed GE was observed in the middle of this last phase.

Relative energy intake:

The adult seals in this study ingested (per month and per year) up to twice the energy predicted from the equations devised by Innes *et al.* (1987) (Table 11). The equations for growing juvenile phocids accurately predicted energy intake for male #4 (up to June 1992; thereafter he was treated as a growing adult and the power of prediction decreased) and male #5.

There was greater agreement between predicted and observed values for the adult seals when using the relationship calculated by Farlow (1976) for carnivorous mammals than with predictions by Innes *et al.* (Table 12). For the female, there was almost no difference between predicted and observed energy ingestion values for 1992 and 1993. However, Farlow's equation was less accurate in representing GE in the two youngest seals, who ingested up to 42% more energy than was predicted.

Discussion:

In the wild, marine mammals may be restricted in their energy intake due to reproductive behaviour (limited time to find prey), moulting ("physiologically restricted" from entering water), endogenous control and prey availability. Some of these factors might not apply to captive marine mammals, as prey availability is certainly not seasonal, and feeding may take place out of the water and within a condensed time period. Yet seasonal fluctuations in energy intake still occur in captive pinnipeds. Further, these variations tend to

Table 11:

Observed GE (per month and per year) as a percentage of that predicted for maintenance by Innes *et al.* (1987). Predictions for males #1 and #2 and the female used the equation predicting ingested energy (GE in kJ/d) from body mass (M in kg) for non-growing, adult phocids: $GE=858.0M^{0.72}$ [equation 8a in Innes *et al.* 1987, converted to appropriate units]. The formula for growing, adult phocids was applied to male #3: $GE=534.82M^{0.80}$ [equation 28]. This same formula was applied to male #4 after June, 1992. Prior to this, the equation for growing, juvenile phocids was applied: $GE=2082.2M^{0.57}$ [equation 30a]. This last formula was consistently applied to male #5.

1991	Male 1	Male 2	Female	Male 3	Male 4	Male 5
June	100.6	88.5	51.3	38.1	107.9	
July	91.4	67.8	109.2	67.5	83.2	
August	214.5	247.9	243.1	163.7	107.6	21.3
September	242.2	176.5	284.4	212.8	116.8	50.2
October	248.6	217.3	247.6	197.8	128.5	108.5
November	183.7	207.2	169.9	142.7	124.6	115.5
December	170.5	175.2	124.5	106.5	118.0	101.0
Annual GE	180.1	166.2	172.7	130.1	111.9	79.31

Table 11 (continued):

1992	Male 1	Male 2	Female	Male 3	Male 4	Male 5
January	131.4	109.1	93.2	96.6	84.5	77.7
February	137.8	148.3	77.4	81.9	84.6	72.9
March	122.2	133.7	57.6	115.6	74.9	69.9
April	197.7	192.2	139.1	152.0	110.2	81.1
May	199.7	224.2	170.9	159.0	130.0	100.5
June	117.6	134.2	107.4	102.8	101.9	123.2
July	138.6	136.7	247.4	171.5	133.4	110.7
August	206.7	241.3	209.9	143.1	88.3	81.3
September	205.2	161.3	206.8	133.7	115.3	85.1
October	151.1	133.4	141.6	88.4	66.9	90.3
November	137.8	179.9	108.7	122.8	86.8	86.8
December	119.4	157.5	96.0	113.6	93.5	84.3
Annual GE	154.8	162.3	134.6	123.5	97.6	88.7

1993	Male 1	Male 2	Female	Male 3	Male 4	Male 5
January	96.8	130.3	85.4	127.5	130.1	92.9
February	150.7	179.7	120.1	142.4	139.7	105.2
March	110.7	163.0	88.0	124.6	118.2	96.2
April	126.1	176.1	62.6	151.8	122.2	93.6
May	106.4	153.1	111.9	111.1	107.9	91.2
June	188.4	157.6	215.3	168.5	159.2	199.3
July	104.2	106.5	107.1	95.1	119.8	69.4
August	189.3	189.0	118.7	146.7	152.5	63.7
September	198.5	159.5	195.2	147.5	157.8	100.6
October	197.4	180.5	170.2	150.4	160.1	108.6
November	196.9	181.3	158.0	144.1	172.4	111.8
December	148.1	131.8	80.4	103.3	151.7	87.8
Annual GE	149.3	158.5	124.7	134.0	138.9	101.3

Table 12:

Observed GE (per month and per year) as a percentage of that predicted by Farlow (1976) for carnivorous mammals. The allometric equation (converted to appropriate units) predicting gross ingested energy (GE in kJ/d) from body mass (M in kg) is: GE = $915.84M^{0.692}$.

1991	Male 1	Male 2	Female	Male 3	Male 4	Male 5
June	69.3	60.9	35.2	32.9	129.5	
July	62.7	46.5	74.5	57.7	99.8	
August	147.0	169.7	165.7	138.6	130.2	30.2
September	166.0	120.7	194.2	179.4	143.1	72.2
October	170.7	148.7	169.7	168.3	157.8	155.3
November	126.2	141.9	116.7	121.6	153.0	161.3
December	117.2	120.3	85.7	91.1	142.6	137.6
Annual GE	123.7	113.9	118.2	111.0	135.7	111.3

1992	Male 1	Male 2	Female	Male 3	Male 4	Male 5
January	90.4	74.9	64.1	83.0	101.6	104.9
February	94.8	101.7	53.2	69.9	101.2	98.2
March	83.9	91.7	39.6	98.7	89.9	93.9
April	135.9	131.8	95.5	129.8	133.1	109.7
May	137.4	154.0	117.6	136.8	155.8	135.9
June	81.0	92.3	73.9	88.5	121.6	165.3
July	95.1	93.6	169.0	146.4	160.6	146.1
August	141.9	165.1	143.4	122.0	107.6	106.5
September	141.0	110.4	141.7	114.4	138.9	110.9
October	104.1	91.4	97.2	75.6	80.5	116.8
November	94.9	123.3	74.7	105.1	105.0	111.7
December	82.4	108.1	65.4	97.5	114.0	108.3
Annual GE	106.4	111.3	92.4	105.7	117.5	117.1

Table 12 (continued):

1993	Male 1	Male 2	Female	Male 3	Male 4	Male 5
January	66.7	89.4	58.7	109.4	158.4	119.3
February	103.8	123.3	82.5	122.3	169.1	135.1
March	76.2	111.9	60.4	106.8	143.0	123.4
April	86.8	121.0	42.9	130.5	147.1	120.1
May	73.4	105.2	76.6	96.1	128.9	116.8
June	129.6	108.4	147.4	145.5	187.6	253.5
July	71.6	73.0	73.4	80.8	101.6	87.8
August	129.8	129.5	81.0	123.6	128.5	80.7
September	136.1	109.1	133.4	124.7	133.3	128.1
October	135.5	123.8	116.6	127.9	135.8	137.4
November	135.5	124.4	108.5	123.9	146.7	140.2
December	102.1	90.5	55.2	89.3	129.8	109.3
Annual GE	102.8	108.8	85.4	114.7	142.3	128.7

correspond with those reported for, or expected from, their wild counterparts.

The seals in this study exhibited two periods of decreased food energy intake: during the winter and the breeding season. A similar result was predicted from a bioenergetic model of adult ringed seals (Ryg & Øritsland 1990). In wild mammals decreased food intake during the breeding season is proposed to be the result of behavioural or endogenous restrictions to feeding (Chapter 9), while during the winter it is assumed to be the result of decreased food availability. Many northern mammals are subject to limited winter food supplies (Underwood 1971; Lyman 1982; Reimers *et al.* 1982), including several species of phocids (Härkönen 1987b; Olesiuk *et al.* 1990; Ryg & Øritsland 1990; Murie & Lavigne 1991).

Most wild male pinnipeds restrict their feeding or fast during the mating period (Stirling 1983; LeBoeuf 1986; 1991). This is due to the constraints imposed by remaining in the breeding area, participating in intrasexual competition, and/or defending territories (aquatic or terrestrial). Unlike some phocid species which remain on land throughout the entire breeding season, male harbour seals spend two-thirds or more of their time in the water. Studies of radio-tagged adult male harbour seals suggest that they probably indulge in limited, opportunistic feeding bouts during this time (Thompson 1988; Thompson *et al.* 1989). Walker & Bowen (1993a) proposed that male harbour seals probably have restricted feeding in the 'premating' phase, but undergo almost complete fasting during the 'mating' phase of the breeding season.

The males in this study exhibited progressively more restricted feeding during the breeding period, commencing prior to the birth of the pup. Although mating does not occur until after the pup is weaned, breeding behaviour (increased agonistic interactions) commenced prior to the birth of the pup, concurrent with the drop in food intake (Chapter 9), similar to the activity pattern seen in wild harbour seals (Sullivan 1982; Thompson 1988; Thompson *et al.* 1989; Perry 1993).

Most phocid females exhibit a "fasting strategy" during lactation (Bonner 1984; Oftedal *et al.* 1987; Costa 1991). Although harbour seal females do not remain hauled out during lactation, the presence of a pup is presumed to partially curtail their foraging time and efficiency. However, it has also been noted that small harbour seal females do not possess sufficient fat stores for complete fasting, and there is strong evidence that foraging effort increases towards the end of lactation (Miller 1988; Thompson & Miller 1990; Bowen *et al.* 1992; Boness *et al.* 1994).

The female in this study showed a greater change in GE during the breeding period than the males. Gross energy intake of the captive female was higher in the weeks preceding birth than in the weeks after, although the decline in food intake commenced prior to parturition. Gross energy intake increased towards the end of lactation, but then fell again when the pup was weaned. A similar pattern has been reported for a captive female grey seal (Kastelein *et al.* 1990b).

The scope of circannual variation in GE displayed by both the female and the males seemed to remain relatively uniform across years, regardless of whether the female produced a pup or not, although the exact timing was slightly displaced presumably because mating occurred earlier in 1993. Kastelein *et al.* (1990b) reported that a captive, pregnant female grey seal also exhibited seasonal variation in energy intake, whether the fetus survived or not, but that the timing of these cycles differed substantially between years she did or did not produce a pup..

Although captive marine mammals have greater access to food supplies during the breeding season than their wild counterparts, voluntary decreases in food intake are still commonly observed. Keyes (1968) reported periods of fasting in numerous marine mammal species during their respective breeding periods. Nordøy & Blix (1988) and Kastelein *et al.* (1990b) reported reduced energy intake during the breeding season for captive grey seals. The former study noted an inverse relationship between energy intake and body mass, similar to that reported by Renouf & Noseworthy (1990; 1991) for harbour seals. Both Lager *et al.* (1994) and Renouf *et al.* (1993) found pronounced seasonal changes in energy intake among captive harp seals. Although Cheal & Gales (1992) observed that changes in food intake in captive bottlenose dolphins were correlated with water temperature, they also noted that the dolphins became inappetant during periods of peak sexual activity. Similarly, the food intake of male captive Steller sea lions dropped dramatically between May and July, when aggression towards humans and conspecifics increased (Kastelein *et al.* 1990a). South American fur seals transplanted to the northern hemisphere exhibited decreased GE during a breeding season which was 6 months out of phase with their wild counterparts (Kastelein *et al.* 1995). These reports lend credence to the suggestion that decreases in GE are facilitated by endogenous control, rather than to food availability (see Chapter 9).

Gross energy intake increased dramatically at the end of the breeding period, in both the female and the males, and then decreased during the late moulting period. Depressed GE during the moult is exhibited by most pinniped species as they spend the majority of their time hauled out of the water due to thermoregulatory considerations (Sullivan 1980; Pitcher & McAllister 1981; Härkönen 1987a; Hindell & Burton 1988). The seals in this study may have had a greater GE than their wild counterparts as they had the opportunity to feed without having to enter the water. Keyes (1968) also mentions fasts during the moult period in unspecified captive marine mammals. Two captive grey seals, however, exhibited no reduction in food intake during the moult (Kastelein *et al.* 1990b). Kastelein and co-workers suggested that the hormones associated with the moult keep seals out of water, but do not suppress their appetite. However, it has also been proposed that physiological adaptations should keep animals inappetant during predictable periods of fasting in order to prevent them from demonstrating the increase in activity associated with hungry animals (Mrosovsky & Sherry 1980; Steffens & Strubbe 1987; Mrosovsky 1990).

Given the hypothesis that circannual variation in GE is at least partially a product of the hormones associated with breeding, it might further be predicted that these patterns would not become evident until the seals were sexually mature. In this study, the 5-year-old (male #4) demonstrated seasonal variation in energy intake, and indications of seasonal variation in GE were apparent for male #5 at 2 years of age. This is contrary to the changes in food intake reported by Kastelein *et al.* (1990b) for two captive grey seals, where significant seasonal changes did not occur until the male was 12 years old, and the female was 11 years. The authors suggested that this variation was correlated to sexual maturity, as this was the same year that successful mating occurred. Kastelein *et al.* (1990a) also found that, while seasonal variation in GE of a captive male Steller sea lion was evident between his 4th and 7th years, it wasn't until his 8th year that a specific pattern emerged. In captive South American fur seals seasonal variation in GE became apparent at 6 years of age (Kastelein *et al.* 1995).

At present, captive data provide the only available information on seasonal changes in GE for marine mammals. There is concern not only in extrapolating the results from captive to wild seals (*cf.* Lavigne *et al.* 1982), but also in comparing data collected from captive seals held under different conditions. It has been proposed that some of this variability can be removed by utilizing data from captive mammals which are fed under 'maintenance' regimes, i.e., receiving energy sufficient to maintain a constant body mass (Kleiber 1975). Such data was used by Innes *et al.* (1987) to make interspecific comparisons between the maintenance requirements of marine and terrestrial mammals. The adult seals in this study ingested up to twice the energy predicted from the equations devised by Innes *et al.* (1987), although the predictions made for juvenile phocids were more comparable. Lager *et al.* (1994) found that the equation by Innes and co-workers underestimated energy intake in juvenile harp seals by 16%.

Part of the discrepancy between the predictions by Innes *et al.* (1987) and the values observed in this study may be explained by the fact that the data used by Innes and co-authors were obtained from mammals on maintenance diets. In order to maintain a constant weight (not a natural characteristic), seals on maintenance diets are likely to have their GE restricted below *ad lib* levels. As the seals in the present study were not held on maintenance diets (as demonstrated by the seasonal and net changes in body mass) it is not surprising that they failed to conform to Innes *et al.*'s (1987) predictions.

More general allometric relationships between energy intake (GE in kJ/d) and body mass (M in kg) have been previously published, with a range of $GE=611M^{0.75}$ - $1296M^{0.68}$ for mammals (Peters 1983, Appendix VIIa). Farlow's (1976) equation for carnivorous mammals represents a moderate value. There was better agreement between predicted and observed values for the adult seals in this study when using Farlow's formula than when using formulae generated by Innes *et al.* (1987). However, the equation reported by Farlow failed to accurately predict energy ingestion in the two youngest seals. This is likely due to the additional energy required for growth, as the data originally used by Farlow was primarily from older mammals. Innes *et al.* (1987) calculated that growing juvenile phocids would consume approximately 93% more energy than non-growing adult phocids, and that growing juvenile pinnipeds required 2.1 times more ingested energy than comparable terrestrial carnivores (the latter may be related to greater growth rates). It is interesting that the mass-specific GE was not dramatically higher for the growing seals in comparison to the adults, considering that growing animals are generally assumed to have elevated metabolic rates (Kleiber 1975) (Chapter 7).

It is apparent that energy intake displayed significant seasonal changes, both as gross energy and in relation to body mass. The large seasonal variation in GE observed in these data highlight the dangers of extrapolating annual estimates from short-term studies. These data are used in Chapter 6 to calculate seasonal changes in available energy to determine the energetic result of concurrent changes in body mass and GE.

Summary:

- The seals demonstrated substantial variation in GE during the year, with annual decreases ranging from 50-90%;
- the female exhibited the greatest yearly variation in GE in any given year (range: 81-91%), regardless of whether she produced a pup or not;
- circannual variation in GE was apparent on both an absolute and mass-specific basis; and
- allometric equations from Farlow (1976) more accurately predicted the relationship between GE and body mass for the adult seals than those from Innes *et al.* (1987) - the opposite was true for the juvenile seals.

Chapter 6 - Calculation of Available Energy

Introduction:

In the previous chapter it was demonstrated that the harbour seals displayed significant seasonal variation in their gross energy intake (GE). One of the aims of this study was to integrate the concurrent changes in GE and body mass (via net production energy, NE_P) into available energy (EA). Calculating EA will make it possible to examine the relationship of other bioenergetic parameters (metabolism, thermoregulation, activity) to the observed cycles of energy conservation and utilization. However, net energy (NE) and not GE is the parameter which contributes directly to EA, and so it was necessary to determine the proper conversion of GE to NE.

Research on other piscivorous vertebrates indicates that energy intake is 20-30% higher than metabolic energy needs (Naumov & Chekunova 1980). The three main avenues of energy loss during the transition from GE to NE are through fecal energy (FE), urinary energy (UE), and the heat increment of feeding (HIF). In most studies, NE has been calculated as a constant proportion of GE, with the estimated conversion factor derived from other work. This chapter utilizes previous research and new empirical data to estimate the extent of losses from GE due to FE, HIF, and UE, and to examine factors which may alter their values.

Fecal energy losses were estimated in the harbour seals through fecal manganese concentrations (Fadely *et al.* 1990). The heat increment of feeding was not measured in the harbour seals, but estimates were constructed from data made available from concurrent studies on captive ringed and harp seals. This information was compared with previously published results to derive an estimate of HIF for the harbour seals. Urinary energy losses were not quantified, but an appropriate estimate of this parameter was garnered from the literature. At the end of this chapter, the resulting estimates of GE, FE, UE, and HIF are used to calculate NE. These values of NE are combined with the estimates of NE_P derived in Chapter 4 to determine EA.

Fecal Energy:

One avenue of energy loss from ingested food is fecal energy (FE), which is comprised primarily of food that passes undigested through the animal. Of minor energetic importance are the secretions into, and cellular debris from, the gastro-intestinal tract. Some studies have examined FE as energy per unit time (egesta rate, defecation rate), but for the purposes of constructing energy budgets FE is more useful when expressed as a percentage of GE, known as assimilation efficiency (AE%) where:

$$AE\%=[GE-FE]/GE \times 100.$$

There are three methods for determining FE. The first entails estimating AE% by comparing fecal and dietary energy contents. The methodological problems associated with this are substantial, but the most important of these is the absolute necessity that all fecal material be collected. In addition, fecal energy (lipid) content may inaccurately reflect AE% due to contributions from endogenous sources (e.g., urine), particularly if lipid concentrations are low.

A second method involves adding indigestible markers (either chemical or radioactive) to the food supply in a known concentration. The concentration of these markers in fecal samples can then be used to estimate AE%. This method has been used in the majority of AE% studies, with chromium sesquioxide (Cr_2O_3) being a common additive. This technique assumes that the marker is mixed evenly in the food supply, is not lost if the animal shreds prey items before ingestion, is not leached out if defecation occurs in the water, and that differential digestion of the marker does not occur. The primary advantage of this technique is that total fecal collection is not necessary.

A third technique uses the ratio of natural markers in the food and feces to determine

AE%. The prime characteristics of such markers are that they must be largely inassimilable and be present in sufficient concentrations to allow accurate measurement of changes. Dietary manganese (Mn^{2+}), a trace element that is needed by mammals in very small quantities (4-50 μg kg^{-1} day^{-1}), has been used as such a marker. Fadely *et al.* (1990) found that estimates of AE% in northern fur seals using Mn^{2+} were no different than those using $^{51}CrCl_3$ (a radioactive marker) or Cr_2O_3. This technique requires only fecal and dietary samples, and many of the problems associated with added markers are avoided.

An independent estimate of AE% was determined for the harbour seals nad compared with a number of estimates of FE and AE% for numerous marine mammals (Table 13). In addition, two potential sources of variation in AE% were examined. First, it has been suggested that the level of GE might affect AE% (Blaxter 1989), an important factor in view of the significant seasonal changes in GE observed in the seals. Increased food consumption has been reported to result in decreased AE% in harp seals (Keiver *et al.* 1984). Data were also examined to determine whether AE% changed with age, as has been suggested for humans and ruminant animals (Blaxter 1989; Piers *et al.* 1992).

Method:

Fecal samples were collected from the tank during cleaning or from the deck on an opportunistic basis, from 17 June 1991 until 27 April 1993. Fadely *et al.* (1990) determined that no significant leaching of manganese occurred when fecal samples were left in sea water for a limited period. In an attempt to identify the origin of fecal samples, small plastic numbered fish identification tags (approx. 16x4x1 mm) were inserted into the gut of some of the herring prior to feeding. The tags were obtained from the Dept. of Fisheries and Oceans and were coated in epoxy cement to deter digestion and to make them negatively buoyant. Fecal samples were checked for identifying tags at the time of collection and during analysis. Unfortunately, many of the tags separated from the fecal sample when deposited in the tank. The origin of other samples could be identified when defecation was observed on the deck, and these were immediately bagged and labeled. The origin of most samples was not discernible, and such samples were identified simply as 'general collection'. In many cases these general collection samples were composed of the combined fecal samples from a number of unknown individuals, obtained from the drained tank. Samples were placed in double plastic bags and stored at -70°C until time of analysis. Samples of herring from the lots fed to the seals were also frozen for analysis of manganese concentration.

Analysis of manganese concentrations in the fecal samples and in the herring were carried out by Dr. J. Lawson (Dept. of Fisheries and Oceans). The methodology was the same as described by Fadely *et al*. (1990), except that laboratory digestion of samples was accomplished with an MDS 2000 microwave digester (CEM Corporation, J. Lawson, pers. comm.).

Assimilation efficiency was calculated using the manganese concentrations in the fecal (C_f) and fish (C_i) samples according to the formula (Fadely *et al.* 1990):

$$AE\%=[1-(C_i/C_f)] \times 100.$$

For those fecal samples where direct estimates of C_i were available, calculation of AE% was relatively simple. Unfortunately, some of the fecal samples derived from fish lots that were not analyzed for manganese concentrations. For these samples, AE% was calculated using a mean manganese concentration (C_i) from all of the analyzed fish samples.

Linear regression was used to determine whether AE% changed with GE. The number of samples from known individuals was small (n=20), and their results were combined. As GE differed significantly among individuals (Chapter 5), it was necessary to compare AE% to a relative measure of energy intake. Relative GE was calculated by determining the gross energy intake for the appropriate individual for the seven days previous to the fecal collection date. This value was then expressed as a percentage of the average weekly gross energy intake for that individual in that year.

The possible relationship between age and AE% was also examined. The correlation between AE% and seal age was tested (all seals combined), and age and relative GE were used in a multiple regression model to predict AE%.

Results:

A total of 53 samples yielded estimates of assimilation efficiencies. Average manganese concentration in all of the fish samples (n=25) was 3.21±1.27 (mean±SD in ppm, wet weight). This value was used to calculate AE% from the unmatched fecal samples prior to 22 December 1992. From this date onwards, a concentration of 3.15±0.78, derived from matched fish samples (n=10), was used. Manganese concentrations in fecal samples were quite variable, averaging 48.69±24.99 ppm. Assimilation efficiencies averaged 92.36±2.81% for all samples (Table 14), and 92.56±4.27% for the 20 samples from identified individuals. However, the 17 June 1991 sample from male #5 was collected when he was still nursing and, when removed from the data set, resulted in an average AE% of 92.27±4.18%.

There was no significant relationship between AE% and relative GE ($F_{1,17}$=0.88, p=0.36, r^2=.05) (Table 15). However, this appeared to be partially due to an anomalous AE% estimate of 77.7% from male #3 (4 November 1992), resulting from an exceedingly low fecal manganese concentration (possibly due to a small fecal sample; J. Lawson, pers. comm.). When this data point was excluded from the analysis there was a statistically significant relationship between AE% and relative energy intake ($F_{1,16}$=8.33, p=0.011, r^2=.35). However, this relationship appeared to be driven largely by a single outlying data point (Figure 13).

The effect of age on AE% could not be determined independently for each seal. As the time frame of AE% determinations was relatively short, any observed individual differences might also reflect seasonal changes in energy intake. Therefore, data from all of the seals were pooled. There was no significant relationship between seal age and AE%

Table 13:

Estimates of assimilation efficiency for various marine mammals. Assimilation efficiency (AE%) was calculated as: (GE-FE)/GE x 100. The diet used by Fausett (1976) consisted of either clams, abalone, crabs, or squid (no difference was reported among any of these diets). Also note that some of the results reported by Costa (1982) were obtained from Fausett (1976). Prime & Hammond (1987) suggested that, as their estimate was based partially upon otolith collection, it was probably an overestimation. Values reported by Nørdoy *et al.* (1993b) are based upon *in vitro* digestion experiments.

Species	Diet	AE%	Source
Harbour seal	Herring	91.2	Ashwell-Erickson & Elsner 1981
	Pollock	96.7	Ashwell-Erickson & Elsner 1981
Crabeater seal	Krill	84	Mårtensson *et al.* 1994a
Grey seal	Herring	92.6	Ronald *et al.* 1984
	Mixed	92.8	Prime & Hammond 1987
Harp seal	Herring	92.5-95.0	Keiver *et al.* 1984
	Shrimp	72.2	Keiver *et al.* 1984
	Crustaceans	81-83	Mårtensson *et al.* 1994b
	Capelin	93-94	Mårtensson *et al.* 1994b
Ringed seal	Herring	97.0	Parsons 1977
Northern fur seal	Herring	90.0	Fadely *et al.* 1990
	Herring	93.0	Miller 1978
	Pollock	90.0	Miller 1978
Sea otter	Mixed	80.9	Fausett 1976
	Clam	83.5	Costa 1982
	Squid	80.9	Costa 1982
Pacific walrus	Herring, clam	92.7	Fisher *et al.* 1992
Minke whale	Herring	92.1	Nørdoy *et al.* 1993b
	Herring	90.0	Mårtensson *et al.* 1994a
	Capelin	95.0	Mårtensson *et al.* 1994a
	Krill	93.0	Mårtensson *et al.* 1994a
	Krill	70.6	Nørdoy *et al.* 1993b

Table 14:

Assimilation efficiency estimated from fecal samples. Assimilation efficiency (AE%) was calculated from manganese concentrations in fecal samples (C_i, ppm) and herring samples (C_f) according to the formula: AE%=$[1-(C_i/C_f)] \times 100$ (Fadely *et al.* 1990). The summary is organized by collection date of fecal sample. 'General' denotes unknown or mixed samples, usually gathered from the bottom of the drained tank.

Date	Sample source	Fecal Mn^{2+}	AE%
17 Jun. 1991	Male 5	169.80	98.11
25 Jun. 1991	General	45.05	92.87
25 Jun. 1991	Female	95.91	96.65
02 Jul. 1991	General	49.45	93.50
22 Jul. 1991	General	37.77	91.49
05 Aug. 1991	General	34.08	90.57
19 Aug. 1991	Male 2	34.89	90.79
22 Aug. 1991	General	31.38	89.76
26 Sep. 1991	General	59.33	94.56
25 Dec. 1991	Male 2	34.89	90.79
23 Mar. 1992	General	43.30	92.58
31 Mar. 1992	General	41.45	92.25
31 Mar. 1992	General	50.06	93.58
13 Apr. 1992	General	80.18	95.99
24 Apr. 1992	General	45.76	92.98
05 May 1992	General	42.68	92.47
11 May 1992	General	43.91	92.68
11 May 1992	General	56.82	94.35
15 May 1992	General	40.22	92.01
25 May 1992	General	43.30	92.58
25 May 1992	General	51.91	93.81
29 May 1992	General	42.68	92.47
02 Jun. 1992	General	40.84	92.13
08 Jun. 1992	General	35.92	91.06
15 Jun. 1992	General	40.84	92.13

Table 14 (continued):

14 Jul. 1992	General	43.18	92.56
21 Jul. 1992	General	49.83	93.55
22 Jul. 1992	General	64.92	95.05
31 Jul. 1992	General	30.13	89.34
31 Jul. 1992	Male 5	40.47	92.06
28 Jul. 1992	General	43.30	92.58
14 Aug. 1992	General	30.13	89.34
18 Aug. 1992	General	38.21	91.59
25 Aug. 1992	General	33.24	90.33
01 Sep. 1992	General	35.31	90.90
13 Sep. 1992	General	31.37	89.76
14 Sep. 1992	General	34.48	90.68
22 Sep. 1992	General	43.17	92.56
04 Nov. 1992	Male 3	14.43	77.73
10 Nov. 1992	Male 4	39.30	91.82
12 Nov. 1992	Male 1	59.12	94.57
19 Nov. 1992	Male 2	37.50	91.43
24 Nov. 1992	Male 4	53.72	94.02
26 Nov. 1992	Male 5	27.29	88.23
01 Dec. 1992	Male 3	42.30	92.40
17 Dec. 1992	Male 4	38.70	91.70
22 Dec. 1992	Male 5	75.34	95.74
05 Jan. 1993	Male 3	56.12	94.40
18 Jan. 1993	Male 5	38.58	91.85
28 Jan. 1993	Male 2	50.57	93.78
29 Mar. 1993	Male 1	135.63	97.68
21 Apr. 1993	Male 1	57.66	94.55
27 Apr. 1993	Male 2	44.03	92.86
	Mean ± SD	**48.69±24.99**	**92.36±2.81**

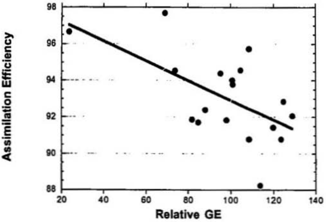
Table 15:

Assimilation efficiency (AE%) compared to weekly GE and relative weekly GE. Data are listed only for fecal samples of known origin, listed in chronological order by collection date. Weekly intake was calculated as GE (MJ/week) in the week prior to the day of fecal sample collection. Relative GE was calculated as the ratio of weekly GE to average weekly GE over that entire calendar year.

Date	Seal	GE (MJ/week)	Relative GE	AE%
12 Nov. 1992	Male 1	23368	104.71	94.57
29 Mar. 1993	Male 1	14878	69.06	97.68
21 Apr. 1993	Male 1	15916	73.88	94.55
19 Aug. 1991	Male 2	25895	123.37	90.79
25 Dec. 1991	Male 2	22805	108.65	90.79
19 Nov. 1992	Male 2	25110	119.81	91.43
28 Jan. 1993	Male 2	21160	100.91	93.78
27 Apr. 1993	Male 2	26134	124.63	92.86
25 Jun. 1991	Female	4950	23.54	96.65
04 Nov. 1992	Male 3	17659	85.38	77.73
01 Dec. 1992	Male 3	18208	88.04	92.40
05 Jan. 1993	Male 3	21435	95.27	94.40
10 Nov. 1992	Male 4	21213	97.94	91.82
24 Nov. 1992	Male 4	21794	100.62	94.02
17 Dec. 1992	Male 4	18362	84.78	91.70
31 Jul. 1992	Male 5	16868	128.89	92.06
26 Nov. 1992	Male 5	14876	113.67	88.23
22 Dec. 1992	Male 5	14211	108.59	95.74
18 Jan. 1993	Male 5	14581	81.90	91.85

Figure 13:

Relationship between assimilation efficiency and relative gross energy intake. Assimilation efficiency (AE%) was calculated from Mn^{2+} concentrations in fecal and fish samples. Relative GE (GE_r) was calculated as the GE for the seven days previous to the fecal collection date expressed as a percentage of the average weekly gross energy intake for that individual in that year. The regression used the samples from known individuals only (Table 15), except for those from 17 June 1991 and 4 November 1992 (see text). The resulting regression equation was: $AE\% = 98.31 - .054GE_r$. While the equation was statistically significant ($r^2 = 0.35$, $p = 0.01$), it appeared to be driven largely by an outlying value ($GE_r = 23.54$, $AE\% = 96.65$).


Assimilation Efficiency
98
96
94
92
90
88
20
40
60
80
100
120
140
Relative GE

with either data from all known samples ($F_{1,17}$=1.85, p=0.19, r^2=.10) or with the AE%=77.7 data point removed ($F_{1,16}$=3.56, p=0.08, r^2=.18). A multiple regression forcing both age and relative food intake variables did account for a statistically significant proportion of the variance in AE% ($F_{2,15}$=6.37, p=0.01, r^2=.43).

Discussion:

A number of factors have been reported to affect AE% in marine mammals, including gender (Fisher *et al.* 1992), condition, and activity (Markussen 1993). Age has been documented to affect AE% in domestic ruminants and humans (Blaxter 1989). In this study, AE% did not appear to change with age, in accordance with results for walruses (Fisher *et al.* 1992) and harp seals (Mårtensson *et al.* 1994b). This was likely due to the small sample size, although it may reflect the precocial nature of young pinnipeds

The estimate of AE% derived in this study was close to the values of 91.2% and 96.7% reported for harbour seals by Ashwell-Erickson & Elsner (1981), and was also well within the range reported for other piscivorous marine mammals. When estimating AE% from published reports, it is important to take diet type into account (particularly if applying data from captive seals to wild individuals whose diet composition is usually more varied). A number of studies have examined FE loss and AE% in marine mammals (Table 13) on various diets, with some studies directly examining the effect of diet type on AE% (Miller 1978; Ashwell-Erickson & Elsner 1981; Costa & Kooyman 1984; Keiver *et al.* 1984; Fisher *et al.* 1992; Nordøy *et al.* 1993b; Mårtensson *et al.* 1994a; 1994b). Overall, AE% is quite high for pinnipeds on a herring diet, ranging from 97% reported for ringed seals (Parsons 1977) to 90% for northern fur seals (Fadely *et al.* 1990). The mean value of 92.4% obtained in the current study is comparable to previously published values for pinnipeds on herring diets, including the value of 91.2% for harbour seals, specifically (Ashwell-Erickson & Elsner 1981).

Energy intake levels may also affect AE%. In ruminants, both increased food mass and increased GE decreases AE% (Blaxter 1989). In the present study there was a poor relationship between AE% and the level of energy intake. Similarly, Keiver *et al.* (1984) and Inman & Smith (1941) found that the level of energy intake did not affect relative fecal energy loss in harp seals and silver foxes, respectively. As the statistical relationship between GE and AE% found in the present study was questionable and only accounted for 34% of the observed variance, it was decided that a mean value of 92.4% would be used as an estimate of AE%.

Although this study does not modify AE% for levels of GE, the possible effects of incorporating such changes into the calculations of apparent digestible energy (DE) are illustrated in the following example. A range of GE of 100-300 MJ/week (annual mean = 200 MJ/week) is fairly typical for the adult seals in this study. Given the relationship AE% = 98.31 - 0.054GE_r (derived from the linear regression, where GE_r is relative gross energy intake), the resulting range of DE would be 95.6-262.5 MJ/week. Using an average AE% of 92.4% yields a similar range in DE of 92.4-277.2 MJ/week.

Urinary Energy:

Loss of energy via urinary excretion of nitrogenous wastes is an immutable part of energy metabolism, whether the energy source is external (i.e., food) or internal body reserves. There is no agreement whether urinary energy (UE) should be expressed as a proportion of GE or DE. As UE is a physiological byproduct of energy that has been absorbed into the system, it is probably more appropriate to express it in terms of DE, although this assumes that FE has also been estimated. Since FE is unknown in most cases, UE is often expressed as a proportion of GE. All studies which have examined UE in marine mammals have utilized collection holding facilities, where all urine must be collected to obtain a reasonable estimate. Many of these studies have also examined FE, so that UE losses can be calculated as a portion of either GE or DE.

Table 16:

Estimates of the cost of urinary energy loss among seals. Urinary energy loss (UE) is presented as a proportion of apparent digestible energy (DE). Values in italics are derived from reported values of UE as a proportion of GE and additional data in the source studies.

Species	Diet	Proportion of DE	Source
Grey	Herring	*10.5*	Ronald *et al.* 1984
Harbour	Herring[1]	*3.2*	Ashwell-Erickson & Elsner 1981
	Herring[2]	*5.3*	
	Pollock[2]	*7.5*	
Harp	High energy herring	6.9	Keiver *et al.* 1984
	Low energy herring	9.5	
Northern fur	Herring	3.3	Miller 1978
	Pollock	2.6	
Ringed	Herring	8.8	Parsons 1977
	Herring[3]	9.8	
	Capelin[3]	7.2	

1. Yearling harbour seal.

2. Four-year-old harbour seal.

3. Same seal alternately fed herring and capelin.

A number of factors have been reported to affect UE. Urinary energy loss depends upon both the dietary protein balance and health of the animal (Brody 1945). The composition of urine is most affected by changes in water intake, although this will only alter urine concentration as opposed to total energy content. A review of the literature for marine mammals (Table 16) suggests that UE loss may be a factor of taxonomy and/or diet composition.

Parsons (1977) found that, for three ringed seals, UE constituted 8.8% of DE (range 5.5 -10.6%) when they were fed herring. The single seal alternately fed herring and capelin had UE losses estimated at 9.8% and 7.2% of DE, respectively. The average energy density of the herring was 8.44 kJ/g, while the capelin averaged only 4.63 kJ/g.

Keiver *et al.* (1984) also found that UE varied slightly with the energy density of the diet in harp seals. Although their original paper reported diet energy densities of 7.04 and 6.32 kcal/g, this would translate into abnormally high energy densities of 29.47 and 26.46 kJ/g, respectively. Assuming that this is a typographical error, their results suggest that UE constituted 6.9% of DE with high-energy density herring (7.04 kJ/g) and 9.5% of DE when fed low-energy density herring (6.32 kJ/g).

This supports findings by Ronald *et al.* (1984) who suggested that UE and nitrogen losses increased with apparent digestible nitrogen intake in grey seals. Their experiments indicated that UE accounted for 7.9% of GE intake. Working from their data (Table 3, their paper), this translates into UE accounting for an average 10.5% of DE.

Ashwell-Erickson & Elsner (1981) estimated that UE constituted 2.9-7.3% of GE in harbour seals, depending on both age and diet. Using their data (Table 53-6, their paper), this translates into UE comprising 3.2% (herring diet, 1 yr old seal), 5.3% (herring, 4 yr old), and 7.5% (pollock, 4 yr old) of DE. Again, the higher energy density herring diet (average = 8.54 kJ/g) resulted in lower UE loses than the lower energy density pollock (4.55 kJ/g). In contrast, Miller (1978) found that juvenile northern fur seals fed either herring or pollock excreted 3.3 and 2.6% of DE as UE, respectively.

Urinary energy losses reported for sea otters appear to be higher than for pinnipeds. Costa (1982) found that sea otters expended 10% of GE as UE. This elevated value may be related to the low AE% also reported for these animals, which may both relate to their rapid food passage rate.

The current study uses the estimate that 5.5% of GE is lost as UE, a value derived from the results reported by Ashwell-Erickson & Elsner (1981). However, the range of figures reported in the literature can provide a rudimentary set of confidence limits to this estimate.

Heat Increment of Feeding:

Early studies on humans revealed the effect of feeding upon oxygen consumption, a phenomenon that was explained by Bidder & Schmidt in 1877 as the 'work of digestion' (Kleiber 1975). Both the mechanical and biochemical processes of digestion increase metabolism, resulting in a 'loss' of energy labeled the heat increment of feeding (HIF). The physiological impact of an animal's absorptive state upon its metabolism was noted by Kleiber (1975) and has also been of concern to those studying the metabolism of marine mammals (for a review see Lavigne *et al.* 1986). However, most studies of marine mammal metabolism have attempted to remove the effect of HIF, in order to more readily make comparisons across some standard physiological condition (see Chapter 7).

Few determinations of HIF have been made for marine mammals. The most common procedure (and the one used to obtain the results reported below) is to measure increases in metabolism (using indirect calorimetry) over some basal, post-absorptive level, having given the animal a quantity of food of known mass and energy content. The increase in metabolism is attributed to HIF and can be calculated as a percentage of GE.

Although no direct measures of HIF were made for the harbour seals used in this study, data from concurrent projects was made available (courtesy of A. Hedd, Memorial

University) that provided an estimate of HIF in 2 captive ringed (Ph1, Ph2) and 3 captive harp seals (Pg1, Pg2, Pg3). In general, the effect of HIF appeared to last from 8-10 hr, with peaks in oxygen consumption occurring about 3-4 hr into the trial (Figure 14). However, there was much individual variation in both the timing of the peak and the duration of the effect.

There was a significant difference between the results for the two ringed seals. The average HIF for the male (Ph1; 9.18±3.72% GE, mean±SD) was twice that of the female (Ph2; 4.45±2.29%; Table 17). There was more consistency within the harp seals tested, with averages ranging from 9.90±3.82% in the adult female (Pg1) to 11.10±1.83% in the adult male (Pg3).

The average estimate of HIF from all of the ringed seal trials (7.08±3.89%, n=9) was lower than that for the harp seals (10.43±4.09%, n=10), although this difference was not statistically significant (Unpaired t=1.826, p=0.23). The overall average HIF, all seals combined (n=19), was 8.84±4.25%, and the grand mean calculated from the independent means of each seal (n=5) was 8.97±2.62%.

Although comparative data are scarce, the results of this preliminary analysis fall within the range of those previously reported for marine mammals. The HIF for the captive ringed and harp seals also appear to be at the lower end of those reported for other mammalian species (see Blaxter 1989, Table 12.1).

Parsons (1977), in a study of two ringed seals, examined the cost of HIF from a single meal "sufficient for maintenance levels". In the two trials reported, the animals showed a 26.9% and 35.0% increase in metabolic rates over daily 'basal' (pre-feeding) levels. Peak effects were reported 4-6 hr after ingestion when metabolism reached 1.8-2.0 times pre-feeding levels, and HIF appeared to last for 12-13 hr post-feeding. Unfortunately, it is impossible to determine the percent of GE lost as HIF with the data provided.

Figure 14:

The effect of the heat increment of feeding on oxygen consumption. The heat increment of feeding was calculated as the difference in observed VO_2 between the control and experimental trials. In this example, the seal (Pg3; see Table 17) consumed herring with a total energy content of 21021 kJ. The increased oxygen consumption was calculated to represent 2443 kJ, resulting in an estimated heat increment of feeding of 11.6% of GE.

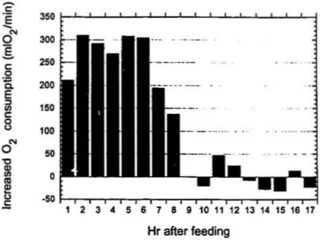

Increased O_2 consumption (mlO_2/min)
350
300
250
200
150
100
50
0
-50
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Hr after feeding

Table 17:

The cost of the heat increment of feeding. The cost of the heat increment of feeding (HIF) is expressed as a percentage of gross energy content of the meal. Results are given for two ringed seals (Ph) and 3 harp seals (Pg).

Subject	Sex, Class	Trials	Range	Mean±SD
Ph1	M, Adult	5	4.1-13.4	9.18±3.72
Ph2	F, Adult	4	2.8-7.8	4.45±2.29
Pg1	F, Adult	2	7.2-12.6	9.90±3.82
Pg2	M, Adult	3	9.5-13.1	11.10±1.83
Pg3	M, Juvenile	5	5.7-19.5	10.24±5.64
Ring Seals		9		7.08±3.89
Harp Seals		10		10.43±4.09
All seals		19		8.84±4.25

Two studies have investigated the cost of HIF in harbour seals. Ashwell-Erickson & Elsner (1981) found that HIF accounted for 4.7% of GE and 5.5% of DE for a yearling harbour seal. Markussen *et al.* (1994) found that juvenile harbour seals (0-4 yr) exhibited different levels of HIF depending on the lipid content of the diet (n=19). Seals fed herring of low-energy density (6.58-8.71 kJ/g) demonstrated a HIF of 9.0 ± 2.8% of GE, while those fed a diet of high-energy herring (10.13-12.56 kJ/g) exhibited an HIF of 5.1 ± 2.3% of GE. The differential effect of diet was also demonstrated in sea otters. Costa & Kooyman (1984) found that sea otters displayed a HIF of 13.2% of GE when fed squid (3.60 kJ/g) and 10% of GE when fed clams (4.98 kJ/g). These results suggest that high-energy diets are more useful to animals since, not only is the energy density greater, but the cost of HIF (as a percent of GE) is less (although AE% may also decrease with energy density).

It has been suggested that HIF should increase curvilinearly with ingested energy (Blaxter & Boyne 1978), as has been demonstrated in sheep (Webster 1981). In the limited data made available for the current study there was no relationship between GE and HIF ($F_{1,17}$=0.392, p=.64). However, it is important to note that the range of GE was quite low (6958-24759 kJ), only about half of the range seen in their normal diet.

Gallivan & Ronald (1981), estimating the effects of meal size on HIF for a single female adult harp seal, found that meals of 1 kg (n=6) and 2 kg (n=2) of herring elevated daily metabolic rates by 11.14 and 20.77%, respectively (measured against a pre-trial, 24 hr starvation period). This translated into a loss of 16.82 and 15.74% of GE through HIF. It should be noted, however, that the cost of HIF for the 2 kg meals may have been underestimated as the metabolism had not quite subsided to baseline levels by the end of the experiment. In addition, the effect of the control (starvation) treatment on 'normal' metabolic levels was not investigated. Markussen *et al.* (1992b) found a substantial depression in metabolic rates within 24 hr of food deprivation in harbour seals.

For the purposes of this study, an intermediate value for HIF of 8.8% was used. This value, derived from the experimental ringed and harp seal data, also falls within the range of diet-specific values reported by Markussen *et al.* (1994) (the energy density of the diet in this study was of an intermediate value to those used by Markussen *et al.*). It is also similar to most other published estimates of HIF for marine mammals, and slightly below the average of estimates for terrestrial mammals.

The range of reported values for HIF can be used to define rudimentary confidence limits. The estimate of HIF used in this study is lower than the figure of 17% of GE used in most bioenergetic models (e.g., Keiver *et al.* 1984; Markussen *et al.* 1992a; Krockenberger & Bryden 1993; Olesiuk 1993), a value obtained from the study of a single individual by Gallivan & Ronald (1981), which would seem to be at the high end of most published estimates. Different estimates of HIF will have a direct impact upon consumption estimates. For example, if Markussen & Øritsland (1991) had used a HIF value of 10% rather than 17%, their estimate of the maximum herring consumed by harp seals in the Barents Sea would have decreased by over 100,000 metric tons per year.

Metabolizable and Net Energy:

The present study assumes estimates of 7.6 and 5.5% of GE lost as FE and UE, respectively. These values translate into 86.9% of GE being made available as metabolizable energy (ME). This compares favourably to a range of 85.5-88.7% given by Keiver *et al.* (1984), a value used in most pinniped bioenergetic models. However, most models use ME and NE interchangeably, thereby discounting the costs of HIF. The present study estimated HIF to comprise 8.8% of GE and, combined with the previous estimates, this results in 78.1% of GE available as NE.

It is possible to combine the range of reported values of UE and HIF with the experimental value for AE% (92.4) from the current study to investigate the range of possible values for converting GE to NE. Minimum values of 2.9% and 4.7% GE lost as

UE and HIF, respectively, have been reported in previous studies of marine mammals, as have maximum values of 9.8% and 17.0%. These estimates result in a range of 65.6-84.8% of GE available as NE. The value of 78.1% used in this study is slightly above the midpoint of this range. The results of these costs on the ingested energy made available to the seals, as well as these approximate confidence limits, are illustrated in Figures 15a, b, c.

Combining Changes in Body Mass and Energy Intake:

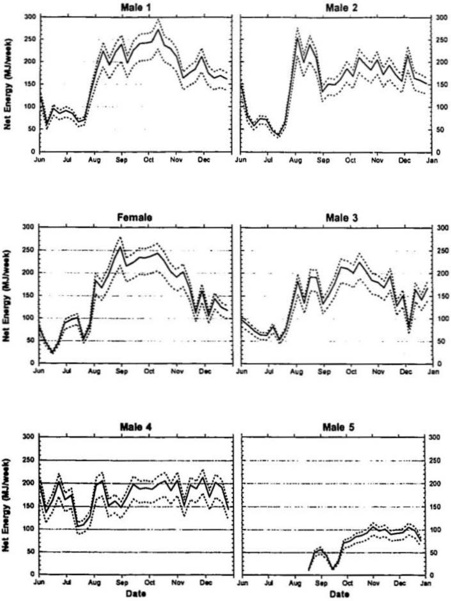
There appears to be no direct relationship between changes in GE and body mass (Figure 16). Renouf and Noseworthy (1990; 1991) noted that, except for a six-week period during Oct.-Nov., these parameters exhibited an inverse relationship. By converting these changes into energetic values, it is possible to estimate the energetic consequences of these concurrent changes. As discussed in Chapter 2, available energy (EA) has been defined as the integration of energy resulting from changes in body mass and composition (i.e., net production energy, NE_P) and GE. This represents the vast majority of the energy utilized by the remaining bioenergetic parameters, including the ones specifically investigated in this study: resting metabolism, thermoregulation and activity.

There is significant variation in available energy during the year (Figures 17a, b, c). Periods when EA is minimal may be regarded as periods of energy conservation in the sense that little energy is attributable to other components of the bioenergetic system. Conversely, times of the year when EA is high may be regarded as periods of high energy utilization. The next step is to investigate other specific components of the seals' energy budgets to determine which factors display seasonal variation that may account for these periods of conservation and utilization.

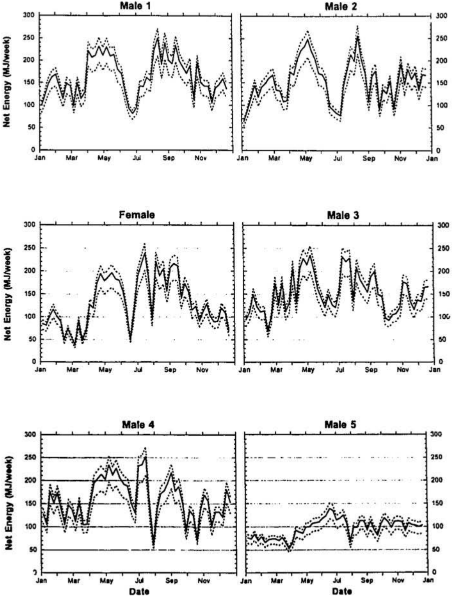
Figures 15a, b, c:

Weekly estimates of net energy. Net energy (MJ/week) was calculated as 78.1% of gross energy intake (GE). The dotted lines represent possible upper and lower limits for net energy, calculated as 84.8 and 65.6% of GE, respectively. Data for the six seals for the three study years are presented separately.

1991


Male 1
Male 2
Female
Male 3
Male 4
Male 5
Net Energy (MJ/week)
0
50
100
150
200
250
300
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Date

1992


Male 1
Male 2
Female
Male 3
Male 4
Male 5
Net Energy (MJ/week)
0
50
100
150
200
250
300
Jan
Mar
May
Jul
Sep
Nov
Jan
Date

1993

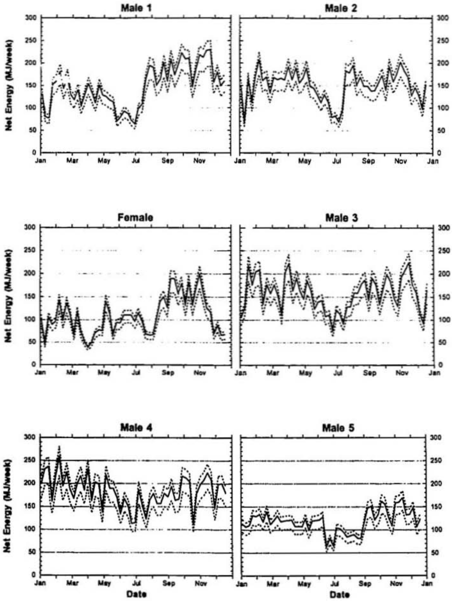
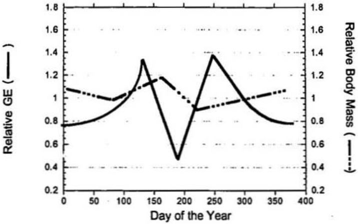

Male 1
Male 2
Female
Male 3
Male 4
Male 5
Net Energy (MJ/week)
0
50
100
150
200
250
300
Jan
Mar
May
Jul
Sep
Nov
Jan
Date

Figure 16:

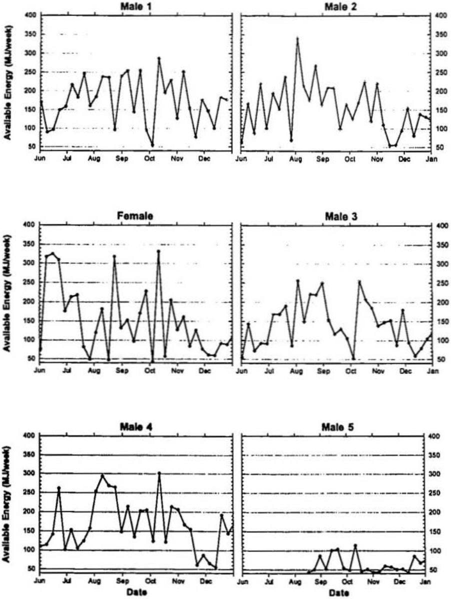
Changes in relative body mass (broken line) and relative GE (solid line) with day of the year. The lines represent the mathematical formulae derived to predict relative body mass and relative GE from day of the year (Table 2 and Table 10, respectively).


Relative GE (——)
Relative Body Mass (—···)
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
50
100
150
200
250
300
350
400
Day of the Year

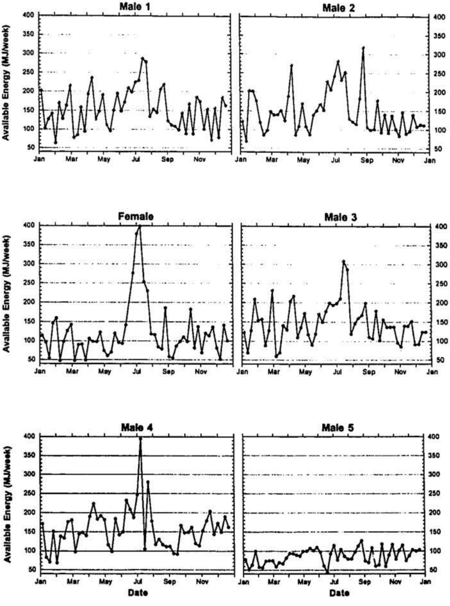
Figures 17a, b, c:

Weekly estimates of available energy. Available energy (MJ/week), was calculated as the difference between production (NE_P) and net energy (NE). Production energy was calculated from changes in body mass and composition and NE was estimated as 78.1% of GE. Data for the six seals in the three study years are presented separately.

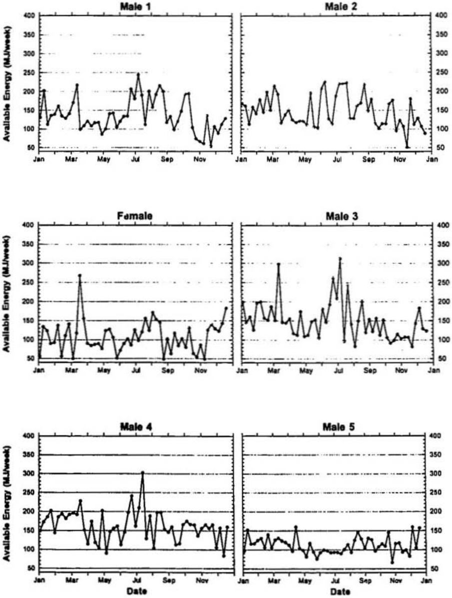
1991


Male 1
Male 2
Female
Male 3
Male 4
Male 5
Available Energy (MJ/week)
400
350
300
250
200
150
100
50
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Date

1992


Male 1
Male 2
Female
Male 3
Male 4
Male 5
Available Energy (MJ/week)
400
350
300
250
200
150
100
50
Jan
Mar
May
Jul
Sep
Nov
Jan
Date

1993


Male 1
Male 2
Female
Male 3
Male 4
Male 5
Available Energy (MJ/week)
400
350
300
250
200
150
100
50
Jan
Mar
May
Jul
Sep
Nov
Jan
Date

Summary:

- Assimilation efficiency, calculated from food and fecal manganese concentrations, was estimated at 92.4%;
- after a review of the literature, a value of 5.5% of gross energy intake (GE) lost as urinary energy was chosen;
- using data from ringed and harp seal experiments, the heat increment of feeding was estimated at 8.8% of GE;
- overall, these values resulted in an estimate of 78.1% of GE available as net energy; and
- circannual changes in net energy and body mass resulted in significant variation in available energy during the year.

Chapter 7 - Seasonal Changes in Metabolism

Introduction:

Interest in the metabolic rates of marine mammals stems from the hypothesis that this group, pinnipeds in particular, survive in their frigid environments by virtue of an elevated metabolism (Irving *et al.* 1935; Hampton *et al.* 1971; McGinnis & Southworth 1971; Irving 1973; Iversen & Krog 1973; Øritsland & Ronald 1975; Lavigne 1982; Innes *et al.* 1987). While estimates of metabolic rates exist for a number of seal species, studies investigating temporal changes in metabolism have generally been limited to the relatively short periods encompassing the breeding or moulting fasts. Yet, in the previous chapters, it was demonstrated that captive harbour seals underwent alternating periods of high energy utilization and conservation throughout the year. It was hypothesized that seasonal changes in metabolism would be an essential adaptation to facilitate the observed long-term changes in energy turnover, and that the captive harbour seals would display significant circannual variation in their metabolic rates.

Changes in environmental temperature and food supplies are two (often concurrent) factors which have been demonstrated to seasonally affect metabolic rates in high-latitude homeotherms. Many non-migratory terrestrial arctic homeotherms experience negative energy balance during the winter due to decreased food availability, at a time when potential thermoregulatory demands are greatest. While elevated metabolic rates are a common physiological response to environmental temperatures outside of a homeotherm's thermoneutral zone, they are not a common adaptation to low seasonal ambient temperatures (Scholander *et al.* 1950a; 1950b; Irving *et al.* 1955; Kleiber 1975; Mrosovsky 1990). On the contrary, polar homeotherms often exhibit depressed metabolic rates in the winter as a mechanism for saving energy, partially as an adaptation to diminished food supplies (Mrosovsky & Sherry 1980; Reinertsen & Haftorn 1986; Stokkan *et al.* 1986;

Prestrud 1991; Schwartz *et al.* 1991; Cuyler & Øritsland 1993).

Many seals have been reported to depress their metabolic rates to conserve energy stores during times of decreased food intake, such as during the moult (Ashwell-Erickson & Elsner 1981; Ashwell-Erickson *et al.* 1986; Castellini & Rea 1992; Rea & Costa 1992; Worthy *et al.* 1992; Markussen *et al.* 1992b; Nordøy *et al.* 1993a). Previous studies have reported large changes in the metabolic rates of harbour seals between the breeding and moulting periods (Ashwell-Erickson & Elsner 1981; Ashwell-Erickson *et al.* 1986). Concurrent with these changes are shifts in plasma thyroxine levels (Ashwell-Erickson *et al.* 1986; Renouf & Noseworthy 1991), a hormone associated with metabolic control. Recent research on captive harp and grey seals suggests that significant changes in metabolism occur throughout the year (Renouf & Gales 1994; Boily 1995; A. Hedd pers. comm.). This chapter examines circannual variation in metabolism in relation to changes in net and available energy.

Documenting seasonal variation in metabolism is important for understanding the energetics of individuals and populations. Estimates of metabolic rates are an essential component in population energetics models (Ashwell-Erickson & Elsner 1981; Øritsland & Markussen 1990; Markussen *et al.* 1992a), and treating metabolism as a constant will reduce their accuracy. Significant seasonal variation in metabolism might necessitate a seasonal parameter to be included in the working definition of standard metabolism.

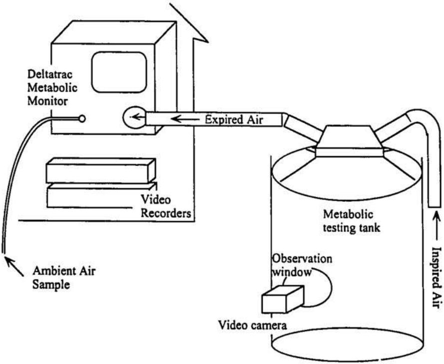
Method:

The metabolic rates of the harbour seals were determined approximately once per month, over a period of 20-24 hr. The first seal was tested 14 July 1992 (after a series of acclimation trials) and the last on 02 November 1993 (Appendix D).

Metabolism was measured using open-circuit gas (indirect) calorimetry. The testing chamber was a circular fiberglass tank (2.5 m high, 1.8 m diameter, 6400 litres), filled with

Figure 18:

Schematic of the experimental set up for metabolic determinations. Metabolism was measured via indirect gas calorimetry, using a flow-through respirometer. The equipment included a 6400 litre testing chamber, two Deltatrac metabolic monitors, and video equipment to record activity.


Deltatrac
Metabolic
Monitor
Expired Air
Video
Recorders
Metabolic
testing tank
Observation
window
Ambient Air
Sample
Video camera
Inspired Air

ambient sea water at the start of each test. The chamber was covered by a lexan and fiberglass respiration hood (volume = 25 litres). The top of the chamber was slanted to ensure rapid collection of expired gases (Figure 18). Air was drawn through the respiration hood at 129-132 l/min, sufficient to avoid an accumulation of expired gases within the hood (specifically, average minute fraction $O_2 < 0.5\%$, $CO_2 < 1.0\%$). Air was drawn by two Deltatrac Metabolic Monitors (Datex Instrument Corp., Helsinki, Finland). The monitors determined O_2 and CO_2 concentrations by paramagnetic and infrared sensors, respectively. Rates of oxygen consumption (VO_2) and CO_2 expiration (VCO_2) were calculated every 2 s and a mean value recorded each min. Before each test the machines were calibrated using a gas of known concentrations (Liquidair Inc., St. John's, NF.). In addition, the flow rates of the Deltatracs were periodically verified using an iron burn method (Young *et al.* 1984).

Prior to each metabolic test, the seals were weighed with either an analog scale (until 20 October 1992, ± 500 g) or digital scale (21 October 1992 onwards, ± 200 g). At the conclusion of each test the data were downloaded to a personal computer. Hourly averages for VO_2 consumption and VCO_2 were calculated, discarding the partial first and last hours from the analysis. Metabolism was measured as the rate of oxygen consumption, but the exact conversion of VO_2 to energy expenditure depends upon the specific energy source used by the animal (Blaxter 1989). However, an average conversion of 1 litre O_2 = 20.1 kJ is the generally accepted mean.

The large number of behavioural and physiological variables that can affect metabolic rates necessitate a standard measurement criterion for comparative purposes (see Lavigne *et al.* 1986). Basal metabolic rate (BMR) is a common comparative measure, defined as the energy consumption of a post-absorptive, mature (non-growing), non-pregnant, quiescent (not active, but awake) individual, tested within its thermoneutral zone (Kleiber 1975). In this study the seals were post absorptive, having not been fed for at least 24 hr prior to metabolic determinations to deter any increases in metabolism due to the heat increment of feeding (Chapter 6). However, the subjects included at least one growing (male #5) and one pregnant seal. Due to these infractions upon Kleiber's (1975) definition of BMR, the term 'resting metabolic rate' (RMR) was used in this study.

Subjects were rarely quiescent for long periods during a test. The seals' natural propensity for activity made it essential to take this metabolic factor into account for comparative purposes. Naturally occurring variation in swimming rates has been used in other studies to estimate 'activity-free' metabolic rates in harbour seals (Markussen *et al.* 1992b; A. Hedd pers. comm.). In the present study, the seals were videotaped from 2000 to 0800 h during each metabolic test through a convex Plexiglas window inset in the side of the tank. A chemical light stick was attached to the hind flipper of the seal with a polypropylene strap so that the seals' movements could be seen at night.

Objective activity scores were based on a 15 min subsample randomly selected from each of the 12 videotaped hr. The scores were linearly regressed against mean hourly O_2 consumption to yield a VO_2 value when activity equaled zero, and the resulting estimate was used as RMR (Figure 19). In most cases these 12 data points provided a significant regression equation. However, in a few cases (such as when a tape failed to record or the image was unclear) the tapes were resampled to obtain a second set of independent, non-overlapping activity scores.

Kleiber (1975) demonstrated that, on an interspecific level, basal metabolic rates (in kJ/d) scaled to body mass (M in kg) in mature, terrestrial mammals according to the formula: $BMR = 293 \times M^{0.75}$ (although see Heusner 1982). Metabolism can be expressed on a mass-specific basis as a multiple to that predicted by Kleiber's equation. For example, metabolic rates of animals with a RMR of twice this predicted value will be denoted as '2.00K'.

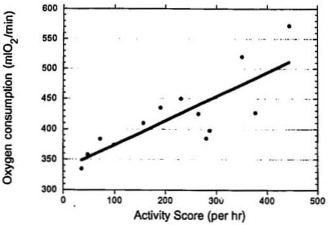
It is important to note that there is a difference in opinion in the literature as to the correct manner to express mass-specific metabolism. It has been suggested that only the core tissue should be considered, as the blubber layer is relatively metabolically inert (Laws 1959; Worthy & Lavigne 1987). Brodie (1975) suggested that using total body mass for marine mammals is equivalent to using body mass plus a considerable portion of its food cache for rodents. However, blubber is not completely metabolically inert, and it does induce a cost of transport (Fish 1992). For the purpose of the present study the more conventional approach, expressing mass-specific metabolism using the seals' total body mass, was used.

Mean annual metabolic rates were calculated from the first 12 months of data for each seal, both on an absolute and mass-specific basis. Estimates of RMR and mass-specific metabolism for each seal were regressed against available energy (EA), net energy (NE), and body mass. These data were also used to determine the effect of age on metabolism. In addition, although it was felt that the seals were not tested outside of their thermoneutral zone, the relationship with air and water temperature was also investigated.

As estimates of mean mass-specific metabolism differed among the adult seals, relative mass-specific metabolism was calculated as the ratio of observed to annual mean mass-specific metabolism. Data from males #1-3 were used to derive mathematical formulae describing circannual variation in relative mass-specific metabolism. As it was more difficult to ascertain a distinctive pattern in the data (partially due to a lower sample size than for other parameters), the relationships derived for mass and energy intake were used as a guideline. The predictive power of the resulting formulae were then tested with two other sets of data, males #1-4 and males #1-3 and the female.

Figure 19:

Method employed to derive resting metabolic rate from oxygen consumption and activity scores. Activity in the metabolic chamber was videotaped from 2000 until 0800 h. Activity was scored for each of these 12 hr and regressed against mean oxygen consumption (mlO_2/min) during that hour. The resulting equation gave a value for oxygen consumption when activity equaled zero. The example given is from a test of Male #2 on 19 November 1992. The regression equation in this example is: $VO_2 = 333.3 + 0.3987 \times$ Activity ($r^2 = .68$), meaning that RMR = 333.3 mlO_2/min.


Oxygen consumption (mlO_2/min)
600
550
500
450
400
350
300
0
100
200
300
400
500
Activity Score (per hr)

Results:

The seals displayed substantial variation in both absolute and mass-specific metabolism over the course of the study (Table 18). Mass-specific metabolism showed a general decline with age among the males, from a mean of 2.08K in the yearling to 1.12K in the oldest male. The annual mean for the female (1.14K) was similar to the latter.

Metabolic rates varied during the year, but all the seals exhibited a similar pattern for both absolute and mass-specific metabolism (Figure 20). Metabolism was highest in April and August, and lowest in June and November. The pattern of seasonal changes in relative mass-specific metabolism were partitioned into four phases, described by mathematical formulae relating metabolism to day of the year (DOY) (Table 19, Figure 21).

Averaged across all seals, there was a 34% decline in mass-specific metabolism from August (average = 1.70K) to November (1.11K) (Table 20). This was followed by a 73% increase from November to April (1.92K). There was a subsequent decline of 31% leading to a low point in June (1.29K), followed by a 21% increase between June and August (1.58K). The mean mass-specific metabolic rate in August 1992 (all seals combined) was slightly higher than the mean obtained the following year.

These changes in metabolism did not appear to be the result of thermoregulatory adjustments to external temperatures. Given that all other parameters remain constant, metabolism should remain constant across a range of external temperatures which define the animal's thermoneutral zone. At upper and lower critical temperatures, metabolism increases and as external temperatures increase and decrease, respectively. As demonstrated in Figures 22 and 23, there was no relationship between metabolism (expressed either in absolute terms or as a multiple of Kleiber's prediction) and either air or water temperature.

There was a stronger relationship between mass-specific metabolic rate and EA than between RMR and EA for three of the seals (for two of these the latter relationship was not significant; Table 21, Figure 24). In two of the seals this trend was reversed (although the

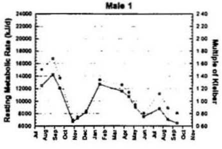
Table 18:

Mass and metabolic rates of the harbour seals. Mean annual metabolic rate ± 1 standard deviation for the period 01 August 1992 to 31 July 1993 are given. For comparative purposes, metabolism is presented in three formats: resting metabolic rate (MJ/d), mass-specific oxygen consumption (mlO_2 kg^{-1} min^{-1}) and as the ratio of observed RMR to Kleiber's (1975) prediction of basal metabolism for adult terrestrial mammals (BMR = 293 x $M^{0.75}$, BMR in kJ/d, M in kg). The ages of the seals as of August 1992 are also given.

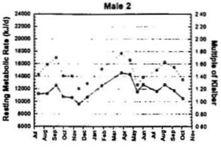
Seal	Age (yr)	Mass (kg)	O_2 consumption (mlO_2 x kg^{-1} x min^{-1})	RMR (MJ/d)	RMR/Kleiber
Male 1	20	99.8 ± 7.0	3.62 ± 1.14	9.92 ± 2.50	1.12 ± .33
Male 2	14	83.9 ± 9.0	4.79 ± 0.63	11.94 ± 1.50	1.43 ± .18
Female	14	82.8 ± 7.5	3.83 ± 0.91	9.00 ± 1.84	1.14 ± .26
Male 3	7	89.2 ± 4.7	4.95 ± 0.81	12.65 ± 2.30	1.50 ± .25
Male 4	6	78.9 ± 5.0	5.58 ± 1.22	12.73 ± 2.09	1.64 ± .34
Male 5	1	49.1 ± 4.6	7.98 ± 1.30	11.14 ± 2.03	2.08 ± .34

Figure 20:

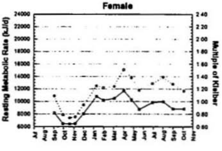
Circannual variation in metabolism. Metabolic rates were measured for the six seals from July 1992 until November 1993. Metabolism is presented both as resting metabolic rate (kJ/d, solid line) and mass-specific metabolism (broken line), calculated as a multiple of Kleiber's (1975) prediction for basal metabolism of terrestrial mammals. Note the scale difference for mass-specific metabolism for male #5.



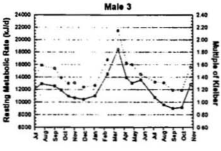
Male 1



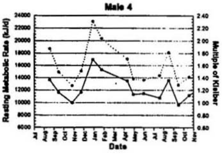
Male 2



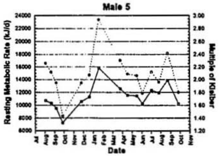
Female



Male 3



Male 4



Male 5

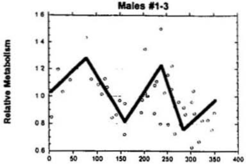
Table 19:

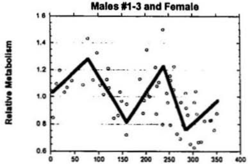
Changes in metabolism with day of the year (DOY). The year has been partitioned into 4 phases, and mathematical formulae derived to express relative metabolism (y) with DOY (x) within each phase. Relative mass-specific metabolism was calculated as the ratio of observed mass-specific metabolism (a multiple of Kleiber's prediction for terrestrial mammals) to mean annual mass-specific metabolism. The formulae were originally derived to describe data from the three oldest males (#1-3), and then applied to data from males #1-4, and males #1-3 and the female. The proportion of the observed variance accounted for by the equation (r^2) is given for each of the data groups for each of the phases. All equations were significant at alpha ≤ 0.01

		Proportion of Variance Explained		
Phase DOY	Formula	Males 1-3	Males 1-4	Males 1-3 + Female
Phase 1				
Day 77-158	$y = 1.7299 - 0.005794x$	.73	.78	.68
Phase 2				
Day 158-238	$y = 0.2588 + 0.003719x$	.21	.19	.20
Phase 3				
Day 238-302	$y = 3.2947 - 0.008718x$	.49	.40	.45
Phase 4				
Day 302-443 (77)	$y = -0.3512 + 0.003682x$	.57	.47	.47

Figure 21:

Changes in relative metabolism with day of the year (DOY). Relative metabolism was calculated as the ratio of observed mass-specific metabolism (a multiple of that predicted by Kleiber) to mean annual mass-specific metabolism. The lines represent the four mathematical formulae given in Table 19, formulated from the data for males #1-3 from April 1991 until June 1992. The three graphs represent three data sets: males #1-3 (top), males #1-3 and the female (middle), and males #1-4 (bottom).


Males #1-3


Males #1-3 and Female

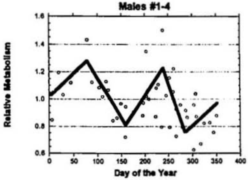

Males #1-4

Table 20:

Seasonal variation in metabolism. Maximum values are given for the periods of August-September and January-March, and minimum values are given for the periods October-November and June-July for the metabolic data from August 1992 to September 1993. Metabolism is presented as resting metabolic rate (kJ/d; upper table) and as the ratio of observed metabolism to Kleiber's (1975) prediction of basal metabolism for adult terrestrial mammals (BMR = 293 x $M^{0.75}$, BMR in kJ/d, M in kg; lower table). The change in metabolism from one period to the next (in italics) is expressed as a percentage of the metabolism of the previous period. Grand means calculated from the averages of the six seals are also given.

Resting Metabolic Rate:

Seal	Aug-Sep	Oct-Nov	Jan-Mar	Jun-Jul	Aug-Sep
Male 1	14264	6738	12635	7556	8828
		-52.7	*+87.5*	*-40.2*	*+16.8*
Male 2	12632	9644	14570	11609	12680
		-23.7	*+51.1*	*-20.3*	*+9.2*
Female	8181	6441	10809	8777	9962
		-21.3	*+67.8*	*-18.8*	*+11.9*
Male 3	12927	10457	18439	10751	9567
		-19.1	*+76.3*	*-41.7*	*-11.0*
Male 4	13669	9998	16967	10785	13601
		-26.9	*+69.7*	*-36.4*	*+26.1*
Male 5	10730	7219	15808	10274	13850
		-32.7	*+119.0*	*-35.0*	*+34.8*
Means		*-29.4*	*+78.6*	*-32.1*	*+14.6*

Table 20 (continued):

Mass-specific Metabolism:

Seal	Aug-Sep	Oct-Nov	Jan-Mar	Jun-Jul	Aug-Sep
Male 1	1.68	0.70	1.34	0.81	0.89
		-58.3	*+91.4*	*-39.6*	*+9.9*
Male 2	1.70	1.21	1.77	1.27	1.63
		-28.8	*+46.3*	*-28.2*	*+28.3*
Female	1.09	0.74	1.25	1.18	1.39
		-32.1	*+68.9*	*-5.6*	*+17.8*
Male 3	1.59	1.30	2.15	1.32	1.31
		-18.2	*+65.4*	*-38.6*	*-0.8*
Male 4	1.88	1.27	2.04	1.36	1.82
		-32.4	*+60.6*	*-33.3*	*+33.8*
Male 5	2.26	1.43	2.94	1.79	2.42
		-36.7	*+105.6*	*-39.1*	*+35.2*
Means	1.70	1.11	1.92	1.29	1.58
		-34.4	*+73.0*	*-30.7*	*+20.7*

Table 21:

Relationship of absolute and mass-specific metabolic rate to available energy, net energy and body mass. Correlations were determined separately for resting metabolic rate (RMR, MJ/week) and mass-specific metabolic rate (Kleiber) calculated as a multiple of Kleiber's (1975) prediction of basal metabolism for adult terrestrial mammals (BMR = 293 x $M^{0.75}$, BMR in kJ/d, M in kg). Correlation coefficients and probability values are given for significant relationships only.

Subject	D.F.	Metabolism	Available Energy (MJ/week)	Net Energy (MJ/week)	Body Mass (kg)
Male 1	12	RMR	n.s.	n.s.	n.s.
		Kleiber	r = 0.62, p = 0.02	n.s.	n.s.
Male 2	14	RMR	n.s.	n.s.	n.s.
		Kleiber	r = 0.51, p = 0.05	n.s.	n.s.
Female	13	RMR	r = 0.61, p = 0.02	r = 0.66, p = 0.01	n.s.
		Kleiber	r = 0.56, p = 0.02	r = 0.52, p = 0.05	r = 0.58, p = 0.02
Male 3	16	RMR	r = 0.58, p = 0.01	n.s.	r = 0.59, p = 0.01
		Kleiber	r = 0.58, p = 0.01	n.s.	n.s.
Male 4	12	RMR	r = 0.54, p = 0.05	n.s.	n.s.
		Kleiber	r = 0.58, p = 0.04	n.s.	r = 0.61, p = 0.02
Male 5	13	RMR	r = 0.60, p = 0.01	n.s.	n.s.
		Kleiber	r = 0.51, p = 0.05	n.s.	n.s.

Figure 22:

Relationship between resting metabolic rate (kJ/week) and air temperature (°C). Data are presented separately for the six seals from July 1992 to November 1993.

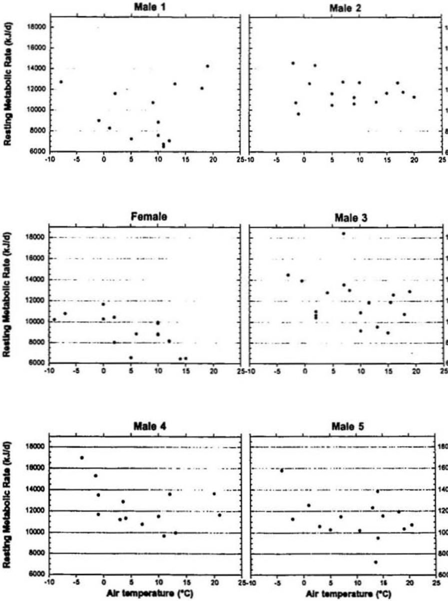

Male 1
Male 2
Female
Male 3
Male 4
Male 5
Resting Metabolic Rate (kJ/d)
6000
8000
10000
12000
14000
16000
18000
-10
-5
0
5
10
15
20
25
Air temperature (°C)

Figure 23:

Relationship between resting metabolic rate (kJ/week) and water temperature (°C). Water temperature was measured in the metabolic chamber at the start of each trial. Data are presented separately for the six seals from July 1992 to November 1993.

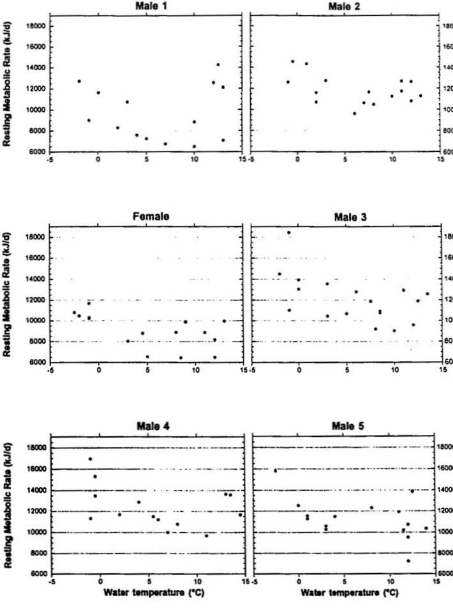
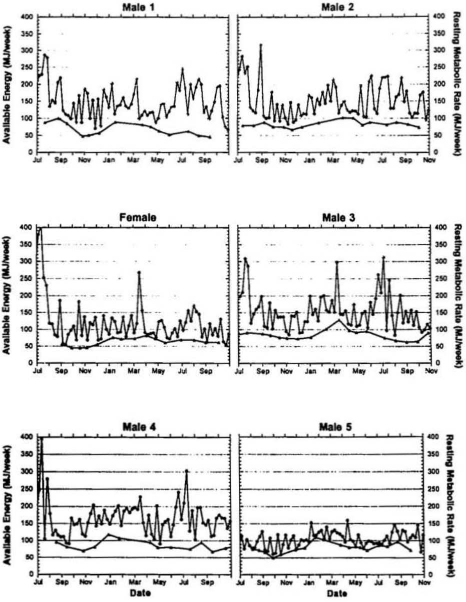

Male 1
Male 2
Female
Male 3
Male 4
Male 5
Resting Metabolic Rate (kJ/d)
18000
16000
14000
12000
10000
8000
6000
-5
0
5
10
15
Water temperature (°C)

Figure 24:

Relationship between resting metabolic rate (MJ/week, open triangles) and available energy (MJ/week, open circles). Data are presented separately for the six seals from July 1992 to November 1993.


Male 1
Male 2
Female
Male 3
Male 4
Male 5
Available Energy (MJ/week)
Resting Metabolic Rate (MJ/week)
0
50
100
150
200
250
300
350
400
Jul
Sep
Nov
Jan
Mar
May
Jul
Sep
Nov
Date

differences were slight), and for male #3 the two measures accounted for an equal proportion of the observed variance in EA. Net energy was significantly related to both measures of metabolism in the female, but neither measure was related to NE in any other seal. Body mass was significantly related to mass-specific metabolism in male #4 and the female, while RMR was significantly related to body mass only in male #3.

Discussion:

Most metabolic studies of phocid seals have been brief, precluding the opportunity to distinguish long-term changes. The results of this study indicate substantial seasonal variation in RMR, superimposed upon an underlying decline with age.

Seasonal variation in RMRs was evident in all seals. As predicted, metabolism was highest during periods of apparent high energy utilization (i.e., high EA) and lowest during periods of apparent energy conservation (i.e., low EA). This pattern is similar to the general changes reported for harp seals (Renouf & Gales 1994).

The lower metabolic rates exhibited early in the breeding season and during the moult occurred during periods when GE was low. Although many studies on phocid energetics have been undertaken during periods of natural fasts or restricted feeding, the effect of decreased energy intake on metabolism is often difficult to ascertain because of concurrent changes in physiology and behaviour (e.g., pupping, moulting, mating, lactation). However, evidence indicates that some species (such as northern elephant and harp seals) lower their metabolism in order to conserve energy stores (Castellini & Rea 1992; Rea & Costa 1992; Worthy *et al.* 1992; Nordøy *et al.* 1993a). In a forced starvation experiment, Markussen *et al.* (1992b) found that the metabolic rates of harbour seals declined by 20% over 16 days, and then returned to previous levels about a week after the onset of feeding. The harbour seals in the present study exhibited low RMRs during periods of hypophagia, indicative of a bioenergetic adaptation to predictable changes in energy intake and demand.

The moult period represents a complex set of energetic demands. During this time the seals have decreased gross energy intake (GE; a result of the seals spending most of their time hauled out of the water - see Chapter 5), which would be predicted to depress RMR. However, the animals are also expending energy toward the refurbishment of their epidermal layer. In addition, harbour seals, unlike some other phocid species, do not spend the entire moult period out of the water. When they do enter the water the energetic cost due to decreased thermoregulatory capabilities may be higher than at other times of the year. It might therefore be predicted that elevated RMRs would be associated with the moult.

Ashwell-Erickson and co-workers found that metabolism dropped significantly during the early part of the moult, and then increased again towards the end (Ashwell-Erickson & Elsner 1981; Ashwell-Erickson *et al.* 1986). A similar pattern was observed in the present study, where RMR decreased 29% during the moult (mass-specific metabolism decreased 34%). These observed decreases in RMR were greater than the 17%-19% reported by Ashwell-Erickson & Elsner (1981) and Ashwell-Erickson *et al.* (1986). Changes in metabolism during the moult are thought to be regulated by hormones, and several studies have demonstrated a relationship between decreasing plasma thyroxine, increasing plasma cortisol and moulting (Riviere *et al.* 1977; Ashwell-Erickson & Elsner 1981; Renouf & Noseworthy 1991).

Although the decreased energy intake during the moult period was associated with depressed RMRs, metabolism was high during the mating period, despite decreased GE. These elevated RMRs were likely related to the increased energy turnover due to reproductive-related activity. There is strong evidence of the high reproductive effort incurred by male harbour seals during the mating period (Thompson *et al.* 1989; Härkönen & Heide-Jørgensen 1990; Thompson & Miller 1990; Walker & Bowen 1993a). Reilly & Fedak (1991) found that the daily energy expenditure (DEE) of male adult harbour seals was 6.00K, or 1.5 times the DEE predicted by Nagy (1987). This period of high energy expenditure and negative energy balance (Reilly & Fedak 1991) may last several weeks (Pitcher 1986; Thompson & Rothery 1987). It is not surprising, therefore, that these periods of increased energy demands were characterized by high RMRs.

The female also exhibited a large decrease in RMR between the reproductive and moult periods. Among phocid seals, the main energy expenditure of females during the reproductive period is assumed to be lactation (Fedak & Anderson 1982; Bonner 1984; Costa *et al.* 1986; Oftedal *et al.* 1987). In the present study, the female continued to exhibit an elevated RMR after lactation had ceased in 1992, and in 1993 when she was not pregnant. The female's elevated RMRs in this study must have been related to other aspects of her reproductive effort (e.g., inter-sexual competition; Chapter 9).

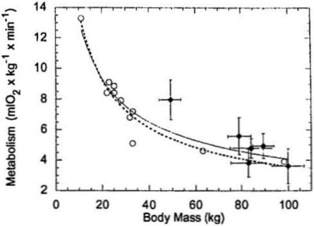
Although it was beyond the scope of this study, it did not appear that the seasonal changes in metabolism were the result of thermoregulatory compensation for changes in external temperatures. Unfortunately, there are no accurate estimates for thermoneutral zones of older harbour seals. However, it does appear that the seals in this study were tested under conditions that were well with the thermoneutral zones of even young harbour seals (thermoneutrality is discussed in greater detail in Chapter 8). In addition, the seals in this study were usually swimming at moderate speeds, which would help to preserve thermoneutrality at lower ambient temperatures.

Underlying these seasonal changes in RMR, there was a general decline in the yearly mean RMR with age, with the mean RMR of the oldest seal (male #1) and the female not significantly different from Kleiber's (1975) prediction of BMR for a terrestrial mammal. Not surprisingly, the RMR of the yearling was twice the value predicted from Kleiber. It is generally accepted that young animals have elevated metabolic rates (Poczopko 1979), but the persistence of this phenomena is unknown. Ashwell-Erickson & Elsner (1981), supplementing their own data with that from Miller & Irving (1975) and Miller *et al.* (1976), suggested a gradual decline in RMR from 2 months of age onwards. A similar

Figure 25:

Relationship between metabolism (mlO$_2$ x kg^{-1} x min^{-1}) and body mass (kg) in harbour seals. The open circles are from a literature review by Rea (1990), as modified by Watts *et al.* (1993). The dotted line represents the relationship calculated from Rea's data: log(Metabolism) = 1.732 - 0.589 log(Mass) (r^2=0.90). The solid diamonds and associated error bars represent the annual mean and standard deviations of mass and metabolism obtained in the present study, summarized in Table 18. The solid line represents the resulting relationship with these points added to those from Rea:

log(Metabolism) = 1.635 - 0.512 log(Mass) (r^2=0.92).


14
12
10
8
6
4
2
0
20
40
60
80
100
Metabolism (mlO$_2$ x kg^{-1} x min^{-1})
Body Mass (kg)

conclusion was made by Rea (1990) after a literature review relating metabolism to body mass in harbour seals. Unfortunately, much of the research on the metabolism of harbour seals has used young animals only. The present study utilized older, heavier seals as well, and appears to confirm the previously observed trends of decreasing mass-specific metabolism with age and body mass (Figure 25). Ashwell-Erickson & Elsner (1981) suggested that declines in metabolic rates were more closely tied to maturity rather than age *per se*. As female harbour seals reach sexual (4 vs. 6 yr.) and physical maturity (6 vs. 10 yr.) faster than males (Boulva & McLaren 1979; Markussen *et al.* 1989), this may explain why the female in the present study had a yearly average RMR equivalent to that of the male 6 years her elder. On the other hand, it may just indicate that changes in RMR with age and mass become asymptotic at an earlier stage.

Mass-specific metabolic rates were found to be more closely related to EA than were RMRs. The stronger relationship between mass-specific metabolic rates and EA suggests that seasonal changes in metabolism were a response to, or facilitated by, concurrent changes in energy turnover, rather than a direct cause of variation in EA. While a large proportion of the variation in EA may be statistically accounted for by seasonal variation in RMR, energetic changes in RMR were minor compared to those observed in EA. Available energy often reached levels of 200-300 MJ/week. However, even the highest estimates of RMR only accounted for 70-100 MJ/week. Therefore, while changes in RMR may directly account for a proportion of the changes in EA, it is likely that they reflect or facilitate other bioenergetic variables which utilize a larger proportion of EA.

Summary:

- Metabolic rates decreased with age, with the metabolic rates of the older seals similar to that predicted for terrestrial mammals of similar size;
- seasonal variation was apparent in both absolute and mass-specific metabolic rates;
- metabolism was elevated during the breeding period and decreased during the moult;
- metabolism was more closely related to available energy than net energy or body mass; and
- metabolism was statistically related to increases in available energy, but changes in metabolism alone did not account for energetic changes in EA.

Chapter 8 - Seasonal Changes in Rectal Temperature

Introduction:

Homeotherms, by definition, are able to maintain internal body temperatures independent of environmental conditions within a wide range of external temperatures. Mean body temperatures are at least partially reflective of phylogeny. Birds typically maintain their body temperatures at 40 ± 2°C, eutherian mammals at 38 ± 2°C, marsupials at 36 ± 2°C, and monotremes at 31 ± 2°C. It was originally assumed that marine mammals, pinnipeds in particular, would have elevated body temperatures as a byproduct of the elevated metabolic rates required to compensate for their environment (Irving *et al.* 1935; Hampton *et al.* 1971; McGinnis & Southworth 1971; Irving 1973; Iversen & Krog 1973). Most research, however, indicates that pinnipeds maintain their internal temperatures at levels typical of eutherian mammals (McGinnis 1968; Ray & Smith 1968; Whittow *et al.* 1971; Ohata & Whittow 1974; South *et al.* 1976; Whittow 1987; Watts 1991).

While homeotherms are able to regulate their temperatures within thermoneutral bounds, this does not imply that deep body temperatures are constant. The core temperatures of many homeotherms display daily fluctuations, reflective of circadian rhythms (Aschoff 1982). Daily changes in rectal temperatures of 1-2°C have been recorded for several species of pinnipeds, including the Hawaiian monk (Ohata *et al.* 1972), the northern elephant (Bartholomew 1954) and the harbour seal (McGinnis 1968; Watts 1991) and the California sea lion (Whittow *et al.* 1971). In addition, the extent of the core tissues which are metaqbolically defended may change in response to thermoregulatory challenges.

Changes in the deep body temperatures of homeotherms have also been found to follow circannual rhythms (Stanier *et al.* 1984; Mrosovsky 1990). Internal body temperatures may vary due to seasonal changes in energy intake, activity, metabolism, or environmental conditions, in either a compensatory or anticipatory manner. For example, in the former, extremes in environmental temperatures may result in additional thermoregulatory costs. Increased energy intake can also result in increased core temperatures through the increased thermal contribution of digestion and assimilation (Parsons 1977; Gallivan & Ronald 1981; Webster 1983; Wilson & Culik 1991; Markussen *et al.* 1994).

When core body temperatures change in an anticipatory manner the deep body set-point (i.e., the internal temperature that is metabolically defended) or the extent of the core area is altered as an adaptive response to predictable seasonal fluctuations (rheostasis; Mrosovsky 1990). Raising the set-point during periods of high energy use would minimize the costs of heat dissipation (Stanier *et al.* 1984; Mrosovsky 1990). Lowering body temperatures during periods of torpor or hibernation (when external temperatures and metabolism are depressed) decreases thermoregulatory demands (Mrosovsky 1990; Geiser & Broome 1993).

No studies have examined long-term changes in the core temperatures of pinnipeds. Yet, seals are subjected to seasonal variation in environmental conditions, and exhibit seasonal changes in energy intake, activity, metabolism, and body composition, all of which could result in changes in body temperature. Given the periods of apparent high and low energy use demonstrated by the present study and those by Renouf & Noseworthy (1990; 1991), it was predicted that the harbour seals would display circannual changes in deep body temperature concurrent with changes in energy turnover.

This chapter examines seasonal variation in rectal temperatures in relation to changes in gross energy intake (GE), available energy (EA), and body mass. In addition, as thermal balance may be influenced by environmental conditions, the relationship between rectal temperature and air and water temperatures was also examined. Among pinnipeds, predictable environmental variables such as changes in light levels (Boyd 1991; Temte & Temte 1993; Lager *et al.* 1994) often serve as entrainment devices (*zeitgeber*) for circannual rhythms. Therefore, the relationship between rectal temperature and minutes of daylight was also explored.

Method:

Weekly measures of deep rectal temperature were taken between 22 April 1991 and 25 May 1992. Rectal temperature was measured to 0.1°C with a digital thermometer and thermal probe (Fisher Scientific, model #A22134) inserted 22.0 cm in the adults and 12.5 cm in the youngest male (#5). Temperatures within the core tissues of homeotherms are not uniform but, for practical purposes, deep rectal temperature can be used as a representative measure. As temperature may change along the length of the colon (Ray & Smith 1968), great care was taken to ensure that the probe was inserted a constant length into the animals.

Due to concern over possible variation in body temperatures due to circadian rhythms or activity, rectal temperatures were taken between 1030 and 1200 h, at the same point in the routine of weekly measurements. This ensured that the seals had been out on the deck and largely inactive for 90 min prior to temperature determinations. The seals were not fed for at least 20 hr prior to the temperature measurements to eliminate any increase in heat production due to digestion and assimilation.

Three measures of environmental conditions were used in this study. Air temperature, measured the same day as rectal temperatures, represented immediate thermal conditions, while average weekly water temperature was used as a measure of long-term seasonal conditions. Air and water temperatures were measured at noon daily using a standard glass laboratory thermometer (±0.5°C). The number of minutes of daylight was calculated from information supplied by Environment Canada (St. John's).

Linear regressions were used to determine the relationship between rectal temperature and six variables: minutes of daylight (day of testing), air temperature (°C; day of testing), water temperature (°C; daily readings averaged over 7 days), GE (MJ/d; daily totals averaged over 7 days), EA (MJ/week; week of testing) and body mass (kg; day of testing). Regressions were determined independently for each seal.

Multiple regression was used to determine the total variance in rectal temperature due to changes in five variables: GE, EA, body mass, and air and water temperatures. The relationship between rectal temperature and minutes of daylight was so poor that it only served to decrease the probability value of the multiple regression by increasing the degrees of freedom, and so was not included in the analysis. Stepwise regressions were also used to test the significance of each of these five components in a predictive model for each seal.

A set of mathematical formulae was derived to describe changes in rectal temperatures in reference to day of the year (DOY) from the pooled data of males #1-3, patterned after the phases used to describe changes in body mass and GE. The formulae derived to describe changes in rectal temperature for males #1-3were applied to the data for males #1-3 plus the female, and males #1-4.

Results:

The four adult males had mean annual rectal temperatures ranging from 36.4-36.5°C (grand mean ± S.D. = 36.5 ± 0.5; Table 22). The female had a mean annual rectal temperature of 36.3 ± 0.6. An ANOVA and Scheffé post-hoc comparisons revealed no significant differences among the mean annual temperatures of the adult seals, and indicated that the youngest male (#5) had a significantly higher mean annual rectal temperature (37.3 ± 0.4) than the adults.

All the seals, except the youngest male (#5), displayed a similar pattern of variation in rectal temperature during the year (Figure 26). Core temperature reached a minimum in early June (start of pupping/breeding), a maximum in August/September (end of breeding/start of moult), with a second, smaller drop in December/January, and a slight rise again in February/March (Figure 27. Mathematical formulae relating changes in rectal temperature to DOY in the adult seals are given in Table 23. The rectal temperatures of the youngest male (#5) displayed no seasonal pattern, but did undergo a gradual, linear decline during the study.

Table 22:

Circannual variation in rectal temperatures. Rectal temperatures (°C) from each of the six seals are presented as annual means ± standard deviation, with annual ranges.

Seal	Mean ± S.D.	Range
Male 1	36.42 ± 0.40	35.3-37.3
Male 2	36.46 ± 0.44	35.3-37.8
Female	36.38 ± 0.42	35.7-37.9
Male 3	36.52 ± 0.50	35.4-37.6
Male 4	36.52 ± 0.49	35.7-38.2
Male 5	37.26 ± 0.49	36.0-38.8

Figure 26:

Weekly measures of rectal temperature. Data are from the six harbour seals for the period April 1991 to June 1992. Note the scale difference for male #5.

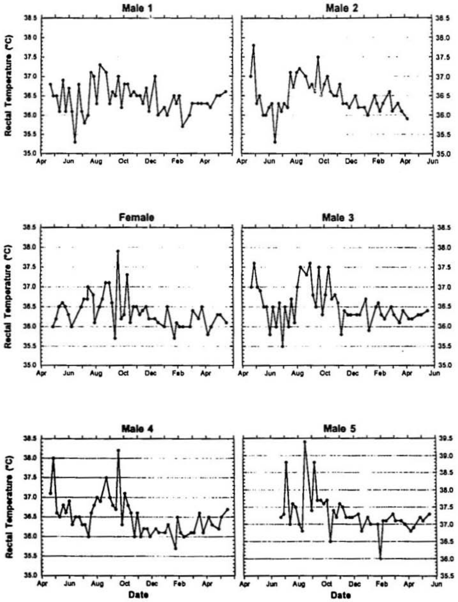

Male 1
Male 2
Female
Male 3
Male 4
Male 5
Rectal Temperature (°C)
Date
35.0
35.5
36.0
36.5
37.0
37.5
38.0
38.5
39.0
39.5
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun

Table 23:

Changes in rectal temperature with day of the year (DOY). The year has been partitioned into four phases, defined by DOY, and mathematical expressions derived to express the relationship between rectal temperatures (y) and DOY (x) within each phase. The formulae were originally derived to describe data from the three oldest males (#1-3), and then applied to data from males #1-4, and males #1-3 and the female. The proportion of the observed variance accounted for (r^2) by the equation is given for each of the data groups for each of the phases.

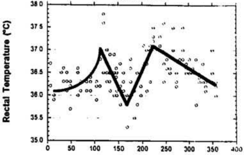
		Proportion of Variance Explained		
Phase/ DOY	Formula	Males 1-3	Males 1-4	Males 1-3 + Female
Phase 1 Day 11-112	$y = 35.61 + 0.046x - 0.0087x^2$	.24**	.23**	.08*
Phase 2 Day 112-168	$y = 39.40 - 0.021x$	.48**	.41**	.39**
Phase 3 Day 168-224	$y = 31.94 + 0.023x$	.59**	.48**	.42**
Phase 4 Day 224-377 (11)	$y = 38.58 - 0.007x$	.46**	.45**	.36**

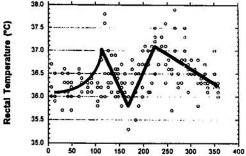
* significant at alpha ≤ 0.05

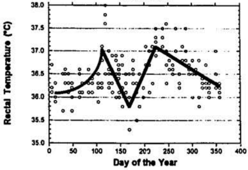
** significant at alpha ≤ 0.01

Figure 27:

Changes in rectal temperature with day of the year. The lines represent the four mathematical formulae given in Table 23, derived from the data for males #1-3 from April 1991 until June 1992. The three graphs represent three data sets: males #1-3 (top), males #1-3 and the female (middle), and males #1-4 (bottom).


Males #1-3


Males #1-3 and Female


Males #1-4

Rectal temperature was negatively related to body mass and positively related to GE (Table 24). Body mass served as a better predictor of rectal temperature than did GE, accounting for a greater proportion of the observed variance in all seals. The relationship between rectal temperature and body mass was significant for all but the youngest seal, and accounted for up to 22.9% of the observed variance. Weekly GE was significantly related to rectal temperature in the four oldest seals, but no significant relationship existed for males #4 and #5. This relationship accounted for no more than 17.3% of the observed variance.

Contrary to initial expectations, EA proved to be a poorer predictor of rectal temperature than either GE or body mass. Available energy was positively related to rectal temperature in males #2, #3, and #4, although it only accounted for a maximum of 7.0% of the observed variance. Available energy was not related to rectal temperature in males #1, #5 or the female.

For all seals, there was a significant positive relationship between water and rectal temperatures, which accounted for 14-26% of the observed variance. Air temperature, although itself closely related to water temperature ($r^2=0.56$, $p<.0001$), was a poorer predictor of rectal temperature. The relationship between rectal and air temperature was significant for only the female and males #1, 4 and 5. For each seal, changes in air temperature accounted for less of the observed variance in rectal temperature than did changes in water temperature. There was no significant relationship between minutes of daylight and rectal temperature for any of the seals.

These results were reflected in the multiple and stepwise regressions. When all five dependent variables were forced into a multiple regression to predict rectal temperature, the full model accounted for up to 61.5% of the observed variance (Table 25). However, the stepwise regression revealed that water temperature was the only consistently significant component of the model. For male #2, GE was also a significant predictor, as was EA for male #3.

Table 24:

Statistical relationship between rectal temperature (y) and air temperature (°C), water temperature (°C), body mass (kg), gross energy intake (MJ/week), and available energy (MJ/week). Regression lines (i.e., rectal temperature = aX + b) are presented for each of the six seals, as well as the amount of observed variance accounted for by the relationship (r^2), and its probability value (n.s. indicates non-significance).

Variable/Seal	Regression Equation	r^2	P-value
Body Mass			
Male 1	$y = -.022x + 38.49$	0.16	.0063
Male 2	$y = -.024x + 38.43$	0.23	.0006
Female	$y = -.013x + 37.49$	0.24	.0006
Male 3	$y = -.032x + 39.25$	0.15	.0090
Male 4	$y = -.026x + 38.53$	0.11	.0243
Male 5	$y = -.007x + 37.83$	0.03	n.s.
Gross Energy			
Male 1	$y = 1.939E\text{-}5x + 35.98$	0.14	.0105
Male 2	$y = 2.229E\text{-}5x + 36.00$	0.18	.0055
Female	$y = 1.484E\text{-}5x + 36\ 10$	0.10	.0420
Male 3	$y = 2.592E\text{-}5x + 35.98$	0.18	.0118
Male 4	$y = 2.291E\text{-}5x + 35.94$	0.03	n.s.
Male 5	$y = 1.776E\text{-}6x + 37.22$	0.00	n.s.

Table 24 (continued):

Air Temperature			
Male 1	$y = .013x + 36.32$	0.08	.0484
Male 2	$y = .010x + 36.38$	0.04	n.s.
Female	$y = .030x + 36.10$	0.22	.0009
Male 3	$y = .009x + 36.45$	0.03	n.s.
Male 4	$y = .023x + 36.34$	0.17	.0038
Male 5	$y = .019x + 37.12$	0.11	.0467
Water Temperature			
Male 1	$y = .034x + 36.27$	0.18	.0031
Male 2	$y = .046x + 36.26$	0.25	.0003
Female	$y = .061x + 36.05$	0.27	.0002
Male 3	$y = .040x + 36.34$	0.15	.0069
Male 4	$y = .046x + 36.31$	0.20	.0014
Male 5	$y = .046x + 37.04$	0.22	.0029
Available Energy			
Male 1	$y = .001x + 36.21$	0.00	n.s.
Male 2	$y = .002x + 36.12$	0.02	.0109
Female	$y = .001x + 36.40$	0.00	n.s.
Male 3	$y = .004x + 35.93$	0.07	.0005
Male 4	$y = .003x + 36.02$	0.02	.0132
Male 5	$y = -.004 + 37.47$	0.02	n.s.

Table 25:

Multiple and stepwise regressions predicting rectal temperature from gross energy intake (MJ/week), available energy (MJ/week), body weight (kg), air and water temperatures (°C). The multiple regression forced all five dependent variables into a predictive model. The resulting proportion of variance that was accounted for by the model (r^2) and the probability value are given. The stepwise regression indicated that water temperature was a significant component of a predictive model in all the seals except male #5. For male #2 and male #3 gross energy intake (GE) and available energy (EA) also constituted a significant component, respectively.

	Mult. Regression		Stepwise Regression		
Subject	r^2	Probability	Components	r^2	F-value
Male 1	.29	.0123	Water	.24	12.477
Male 2	.62	<.0001	Water + GE	.55	24.813
Female	.36	.0047	Water	.33	19.652
Male 3	.51	<.0001	Water + EA	.43	16.983
Male 4	.47	.0002	Water	.42	29.707
Male 5	.29	n.s.	None	n/a	n/a

Discussion:

The rectal temperatures of the harbour seals displayed a considerable circannual variation of 2-2.8°C. These changes were assumedly in addition to the daily fluctuations of between 1°-2°C that have been reported for several pinniped species (Bartholomew 1954; Whittow *et al.* 1971; Ohata *et al.* 1972), including the harbour seal (McGinnis 1968; Watts 1991).

The mean annual rectal temperatures of the adult seals were slightly lower than those previously reported for harbour seals, but were within the range of those reported for most pinnipeds (Table 26). As expected, rectal temperatures were higher in the youngest male (#5) than in any of the adults. Most young mammals exhibit elevated deep body temperatures (Poczopko 1979), which also appears to be true of very young pinnipeds (Bartholomew 1954; Bartholomew & Wilke 1956; Ray & Smith 1968; McGinnis & Southworth 1971; Miller & Irving 1975; Miller *et al.* 1976). While elevated temperatures have been recorded in very young pups, it is noteworthy that male #5 continued to exhibit this feature at two years of age.

It is also noteworthy that the rectal temperatures of the seals in this study (along with those listed in Table 26) fell well within the range of observed values for other mammals, adding support to the hypothesis that seals do not possess elevated core body temperatures (Øritsland & Ronald 1975; Lavigne 1982). It has been suggested that marine mammals exhibit elevated deep body temperatures and metabolic rates in response to the cold environmental conditions they are subject to. Scholander *et al.* (1950a) suggested that an animal may adapt to low temperatures by: 1) increasing heat production; 2) reducing thermal conductance; and 3) reducing the temperature gradient between the body and the environment.

As to this first suggestion, high-latitude mammals rarely increase their heat production through either increased metabolism or activity in response to decreased environmental

Table 26:

Reported values for rectal temperature, in both air and water, for various pinniped species. Data are presented for seals of various age classes (listed by stage, age, or mass) under various testing conditions. Those data listed without specific environmental conditions were tested in air of an unreported temperature. Results from this study are given separately for male #5 (yearling) and all other adults. All temperatures are in °C.

Species	Age/Mass	Air Temp	Water Temp	Body Temp	Source
Harbour	newborn	5-16		37.8	Miller & Irving 1975
	12.6-14.2 kg		19.7-25.0	37.7-38.1	Miller *et al.* 1976
	yearling	-13.1-28		37.3	This study
	98 kg	21.4		37.1	Matsuura & Whittow 1973
	adult	26.1	23.8	37.6	Ohata 1972
	adult	26.1	23.8	36.9	Ohata 1972
	adult	-13.1-28		36.3-36.5	This study
Harp	newborn			36.3-36.6	Blix *et al.* 1979
	white coat	0-4.5		37.1-38.2	Øritsland & Ronald 1973
	157 kg		1.8-28.1	36.2	Gallivan & Ronald 1979
Hawaiian monk	107 kg	27.3	24.0	36.8	Ohata *et al.* 1972
Weddell	pup	-9.5-3.2		37.0	Kooyman 1968
	pup			37.0	Ray & Smith 1968
	adult	-9.5-3.2		36.7	Kooyman 1968
	adult			37.9-38.5	Kooyman *et al.* 1980
Northern elephant	pup	11-22		36.4-37.4	McGinnis 1975
	young			36.0	McGinnis & Southworth 1971
	adult	13.9-16.9		33.8-35.9[1]	Bartholomew 1954
	adult	17.0		35.7	McGinnis 1975
	adult			35.0	Hubbard 1968
California sea lion	pup			38.6	Bartholomew & Wilke 1956
	28.2 kg	20.3		37.8	Matsuura 1972
	32.6-37.0 kg	15-20		37.3-37.7	South *et al.* 1976
	62.2 kg	21.1		37.1	Matsuura 1972
	adult	10		36.5	Whittow *et al.* 1975
	adult	30		38.7	Whittow *et al.* 1975
Northern fur seal	pup	12		38.3	Ohata & Miller, 1977
	pup	12.4		38.2	Bartholomew & Wilke 1956
	3-5 yr	6		37.5-38.9	Irving *et al.* 1962
	juvenile			36.0[2]	Irving *et al.* 1962
	adult	8-9		37.7[3]	Bartholomew & Wilke 1956
	adult	6		38.2-38.5	Irving *et al.* 1962
	adult			38.8	Hubbard 1968
	adult			34.6-40.6	McGinnis 1968

1. reflects night and day shift
2. sleeping
3. driven

temperatures. These parameters usually decrease as ambient temperatures approach some lower critical level (Irving *et al.* 1955; Irving 1972; Stanier *et al.* 1984). However, this does not mean that activity does not affect core temperatures. In the short term, pinnipeds can theoretically reduce core body temperatures while diving (Scholander *et al.* 1942; Scholander 1964; Kooyman *et al.* 1981; Hindell *et al.* 1992; although see Gallivan & Ronald 1981). Long-term changes in rectal temperatures resulting from overall changes in activity levels have been proposed as the major cause of variation in deep body temperature in Hawaiian monk seals (Ohata *et al.* 1972), northern elephant seals (McGinnis & Southworth 1967; McGinnis & Southworth 1971), northern fur seals (Bartholomew & Wilke 1956), and California sea lions (Whittow *et al.* 1971; Matsuura & Whittow 1973; Whittow *et al.* 1975; Thompson *et al.* 1987).

The highest rectal temperatures recorded for the adult seals in the current study were observed during the mating period. There is strong evidence to indicate high energy expenditure among wild adult male harbour seals during the mating season, and it might be suggested this activity produces elevated rectal temperatures. However, it should be noted that the elevated temperatures exhibited by the captive seals were probably not due to an immediate effect of activity, as the animals were quiescent prior to the temperature determinations. Therefore, if activity did contribute to an elevated rectal temperature, it was most likely through an increase in the deep body set-point as an adaptation against the costs of heat dissipation (Stanier *et al.* 1984; Mrosovsky 1990).

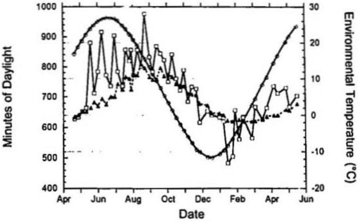
Scholander *et al.*'s (1950a) second suggested mechanism, reducing heat dissipation through decreased thermal conductance, is a winter adaptation exhibited by many high-latitude mammals. For terrestrial mammals this is accomplished primarily by increasing the insulative value of the fur (Scholander *et al.* 1950a; 1950c). Fur pelage shows little seasonal variation in seals, and its role in seasonal changes in insulation is likely minor due to the fact that fur has decreased insulative effectiveness when wet (Scholander *et al.* 1950c). Rather, seals decrease their thermal conductance through increases in the insulative subcutaneous blubber layer (Chapter 4), which has the insulating capacity of asbestos (Bryden 1964). In addition, pinnipeds are able to alter thermal conductance through the processes of vasodilation and vasoconstriction (Irving 1969; Tarasoff & Fisher 1970; Irving 1973; Molyneux & Bryden 1975), wich also effectively alters the extent of the metabolically defended core tissues.

Rectal temperatures were significantly related to water temperatures, perhaps suggesting that the observed changes in the former were a reflection of insufficient thermoregulatory capabilities. However, air temperatures were not a good predictor of rectal temperatures, contrary to what would be predicted if changes in the latter were a result of immediate thermoregulatory demands. It is unlikely that either excess or insufficient insulation was a factor. Although there are no firm estimates of critical temperatures for adult harbour seals (Iversen & Krog 1973; Miller & Irving 1975; Miller *et al.* 1976; Watts *et al.* 1993; Hansen *et al.* 1995) the environmental temperatures experienced in this study do not appear to be extreme. Even newborn harbour seals are able to maintain thermoneutrality in 0°C water (Miller *et al.* 1976). Observed rectal temperatures were highest in June when mass (and insulation) was lowest, but both air and water temperatures were quite moderate. In the winter months rectal temperatures decreased, contrary to the physiological response one would predict for a homeotherm with insufficient insulation. Blubber depth along the trunk did not fall below 2 cm, thereby retaining the theoretical minimum layer needed to maintain thermoneutrality (estimated between 1.5 and 2 cm; Drescher 1980; Hokkanen 1990).

The third adaptation suggested by Scholander *et al.* (1950a) for reducing heat loss under cold conditions is to decrease the thermal gradient between the body and the environment. In its simplest form, the relationship between environmental (T_a) and body temperatures (T_b), thermal conductance of the animal (C), and metabolism (M) may be stated as: $M = C(T_b - T_a)$ (Scholander *et al.* 1950b). One method by which the seals could reduce

Figure 28:

Environmental conditions between April 1991 and June 1992. Data are presented for weekly average water temperatures (solid triangles), air temperatures (open squares), and the total minutes of daylight per day (open circles).


Minutes of Daylight
1000
900
800
700
600
500
400
Environmental Temperature (°C)
30
20
10
0
-10
-20
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Date

thermoregulatory costs is by altering their core temperatures on a seasonal basis. Water temperature was a better predictor of rectal temperature than air temperature, which represented immediate thermal conditions. The former, because of its relative stability, changed in a more predictable manner over the course of the year, and more clearly defined seasonal patterns (Figure 28). This suggests that the seals altered their core temperature set-points during the year in response to predictable seasonal changes in environmental temperatures. Altering set-points would reduce the thermal gradient, and thereby limit thermoregulatory costs (Whittow *et al.* 1971; Mrosovsky 1990; Geiser & Broome 1993).

This hypothesis is supported by evidence that harbour seals modify their thermoneutral zone on a seasonal basis (Hart & Irving 1959; Irving 1969; Miller *et al.* 1976). Seals may also alter the temperature gradient by behavioural adaptations which limit heat loss in air (e.g., snow lairs, body position relative to wind, position within haul out group) (Irving 1969; Ohata 1972; Whittow *et al.* 1975; Hokkanen 1990). Behavioural adaptations might also include changing the amount of time spent in the water (Watts 1992). The benefits of water as a heat sump for seals subject to high environmental temperatures has long been recognized; heat dissipation from a submerged mammal is about 25 times greater than in air (Ridgway 1972). However, as sea water does not fall below -2°C, there will be a point in winter when the higher temperature of sea water compared to the air will result in a lower thermal gradient, despite its higher conductance.

There was a statistically significant relationship between rectal temperature and GE in the older seals. The effect of decreased food intake upon metabolism and body temperature in phocid seals is often difficult to ascertain because of concurrent changes in behaviour and physiology (e.g., pupping, moulting, mating, lactation). However, evidence indicates that some species (such as northern elephant, harp and harbour seals) lower their metabolic demands, and possibly their deep body temperatures, in order to conserve energy stores (Ashwell-Erickson & Elsner 1981; Ashwell-Erickson *et al.* 1986; Castellini & Rea 1992;

Rea & Costa 1992; Worthy *et al.* 1992; Markussen *et al.* 1992b; Nordøy *et al.* 1993a). Conversely, increasing deep body set-points during times of high activity and energy use will decrease the energy needed to dissipate metabolic heat (Whittow *et al.* 1971; Geiser & Broome 1993).

Changes in body mass accounted for a greater amount of variation in rectal temperature (although only up to 22.9%) than GE. The concurrent changes in GE and body mass makes causal determinations difficult, and so it might be more relevant to examine changes in rectal temperatures in relation to changes in EA (the energetic result of changes in GE and body mass). During the breeding and late winter periods the seals lost mass despite an increase in GE, resulting in an increase in EA. This period of increased energy turnover was mirrored by changes in the seals' metabolic rates (Chapter 7) and by a similar rise in rectal temperature. Mrosovsky (1990) suggested that deep body temperature set-points rise as an adaptation to minimizing the costs of heat dissipation. The increased temperatures seen in the present study may have been an adaptive response to increased energy turnover, although the poor relationship between EA and rectal temperatures makes this doubtful.

In the spring and fall, when the seals gained weight despite a reduction in energy intake (low EA), they exhibited a drop in rectal temperature. Decreases in body temperature are a common adaptation among high-latitude homeotherms to decreased energy intake (Hudson 1973; Mrosovsky & Sherry 1980; Lyman 1982; Mrosovsky 1990). It is difficult to determine whether the observed shifts in rectal temperatures were the result of a controlled change in deep body set-points in response to changing energetic demands, or a reflection of changes in heat output due to varying rates of energy turnover. The poor relationship with EA makes the former more likely.

It is evident that the core temperatures of harbour seals exhibited a circannual rhythm. It is difficult to determine the degree to which changes in rectal temperatures facilitated, or were merely a response to, changes in the seals' energy consumption, physiology, behaviour, or environment. Statistically, changes in rectal temperatures were not significantly related to changes in EA. Energetically, changes in rectal temperature will only impact upon EA when the seal is outside of its thermoneutral zone, resulting in increased metabolic costs. The fact that rectal temperatures exhibited a poor relationship to EA provides additional evidence towards the hypothesis that the changes in metabolism described in Chapter 7 were not the result of additional thermoregulatory costs. However, seasonal changes in rectal temperature still constitute an important factor when examining seasonal changes in phocid energetics.

<u>Summary</u>:

- The adult seals displayed a circannual variation in rectal temperature of 2-2.8°C;
- rectal temperature was more closely related to long-term water temperature than immediate air temperature;
- rectal temperature was more closely related to GE than body mass; and
- rectal temperature was not significantly related to EA.

Chapter 9 - Seasonal Changes in Activity

Introduction:

It has been estimated that the costs of activity increase daily energy consumption in wild animals by a factor of 2-3 (Kirkwood 1983; Hui 1987; Harvey *et al.* 1991; Koteja 1991; Karasov 1992). Previous studies have examined the effect of different levels of activity upon food intake or body composition changes in seals on an interspecific (Innes *et al.* 1987; Boyd *et al.* 1993) and intraspecific basis (Anderson & Fedak 1985; Boyd & Duck 1991). It was proposed that changing levels of locomotor activity might account for the variation seen in available energy (EA) in the present study.

Although activity would seem to be the component of the energy budget most under voluntary control, it has been suggested that seasonal differences in the activity levels of northern homeotherms are regulated by both photoperiod and endogenous factors (Stokkan *et al.* 1986). Increased levels of activity are often a response to hunger (LeMagnen 1985) or decreased body mass (Stanier *et al.* 1984; Steffens & Strubbe 1987), serving as a mechanism to motivate feeding. However, Renouf & Noseworthy (1990) found an inverse relationship between activity levels and food intake among captive harbour seals.

High levels of activity may also preclude the opportunity to feed, such as during the mating season. In seals, increases in activity due to inter- and intrasexual competition are supported by the utilization of olubber reserves, thereby decreasing body condition. At other times of the year, this decrease in condition would trigger foraging behaviour. However, it has been proposed that the body fat set-point is lowered during these predictable periods of low food intake to facilitate high levels of activity despite declining energy reserves (Mrosovsky & Sherry 1980; Sherry 1981). This would allow the seal to be in negative energy balance without feeling hunger. The mechanism is similar to that of the 'fight or flight' response, where the sympathetic nervous system curtails digestive processes, promotes breakdown of energy reserves, and diverts blood towards the cardiac, respiratory, and musculatory components.

This chapter evaluates the proportion of variation in EA that was accounted for by changes in activity. Unfortunately, it is difficult to quantify the cost of locomotor activity, particularly in marine mammals, and so this chapter is limited to examining the statistical relationship between these two variables. This will indicate whether the observed energetic changes in EA were likely the result of changes in the seals' activity levels.

Method:

The locomotor activity of the seals in the holding compound was recorded between 0730 and 0930 h from an overhead viewing platform. The seals were each observed for five min in a random order. The main tank and deck area were both divided visually into four sections, and the smaller tanks into halves (Figure 1), and a single activity score was given to the seal when it moved from one section into another. The scores were recorded so that the location and the amount of activity in each location (e.g., deck vs. tank) were known. As a rough conversion factor (to account for differences in distance and effort), a score of 1 on the deck was arbitrarily equated to a score of 4 in the water.

Activity scores were calculated weekly between 14 July 1991 and 26 September 1992, with the following exceptions. From 09 July 1992 until 22 August 1992 activity scores were recorded three times daily (morning, 0730-0930 h; noon, 1230-1330; afternoon, 1530-1700), between 1-3 days a week. This data was used to determine if activity scores varied at different times of the day. Activity scores for male #5 were not recorded until 02 September 1991.

Linear regressions described the relationship between EA and activity scores and also estimated the proportion of observed variance in EA due to changes in activity scores (morning scores only). A mean score was used for weeks when more than one morning activity score was recorded. Relationships were determined between activity score and EA independently for each seal, and between mean EA and mean activity score for males #1-4, combined. The relationship between gross energy intake (GE) and activity scores was also examined for each seal.

A single-factor within-subjects ANOVA was performed on the July-August 1992 data to determine if there was a significant effect of time of observation on activity score. To complete this design (and because changes in activity scores across days was already examined), mean scores across all of the observation days were used from each of the seals (except for male #5), for each of the three observation conditions (morning, noon, afternoon).

Results:

Activity scores were relatively stable from December to June, but they exhibited considerable variation during the other half of the year (Figure 29). For males #1-4, activity increased during the breeding season into the early part of the moult, from mid-June until early August. This was followed by an abrupt decline in activity during the later part of the moult. Activity scores peaked rapidly during the first two weeks of September, and again in mid-October. A similar pattern of activity was exhibited by the female, except during the breeding season. The female exhibited extremely low activity scores during the first part of the breeding season (after the birth of the pup). Activity scores only peaked towards the end (early August) after the pup had been weaned. In contrast, male #5 exhibited variable activity scores from September 1991 until June 1991. Activity was low during the breeding season, peaked dramatically in August, and then returned to previous levels in September 1992.

Available energy was positively related to activity scores in males #1-4, accounting for between 38-45% of the observed variance (Table 27, Figure 30). The regression equation

Figure 29:

Weekly activity scores during the year. Data are presented for the six seals from July 1991 until September 1992.

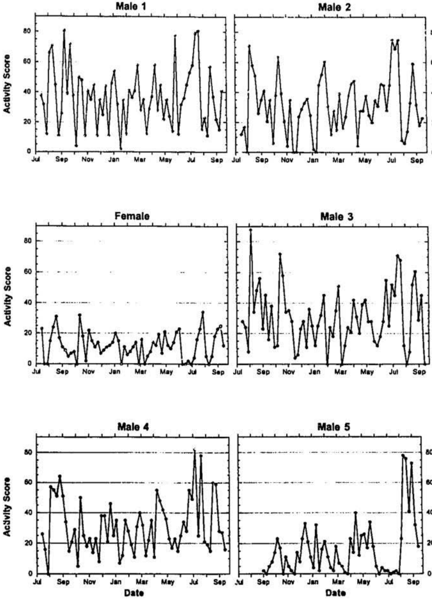

Male 1
Male 2
Female
Male 3
Male 4
Male 5
Activity Score
Activity Score
Activity Score
0
20
40
60
80
Jul
Sep
Nov
Jan
Mar
May
Jul
Sep
Date
Date

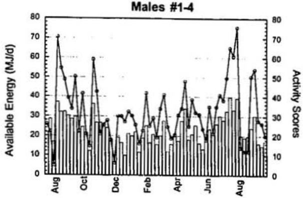
Table 27:

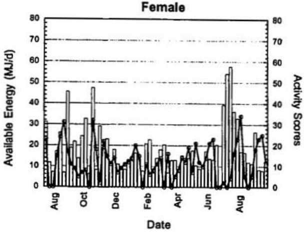
Relationship between available energy and activity scores. Linear regression equations predicting available energy (MJ/week) (y) from activity score (x) (i.e., EA = a + b[Activity]) are given. Also listed is the amount of explained variability (r^2), and the probability value of the equation. Results are presented for the six seals, plus those using mean values from males #1-4.

Seal	Regression equation	r^2	Probability value
Male 1	y = 101.96 + 1.817x	0.38	<.0001
Male 2	y = 91.95 + 2.156x	0.43	<.0001
Female	n.s.	0.02	n.s.
Male 3	y = 94.68 + 1.964x	0.45	<.0001
Male 4	y = 90.39 + 2.318x	0.38	<.0001
Male 5	y = 72.90 + 0.333x	0.07	.046
Males 1-4	y = 73.08 + 2.724x	0.69	<.0001

Figure 30:

Relationship between activity scores (open circles, line) and available energy (MJ/d; vertical bars). Mean values are presented for males #1-4 (top) and for the female (bottom).


Males #1-4
Available Energy (MJ/d)
Activity Scores
0
10
20
30
40
50
60
70
80
Aug
Oct
Dec
Feb
Apr
Jun
Aug


Female
Available Energy (MJ/d)
Activity Scores
0
10
20
30
40
50
60
70
80
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Date

between mean activity scores and mean EA averaged across males #1-4 accounted for 69% of the observed variance. There was a statistically questionable relationship between activity and EA for male #5, which only accounted for a small proportion of the observed variation (7.3%). The relationship between activity and EA was not statistically significant for the female. Linear regressions between activity scores and GE were not significant for any of the seals except male #3, for whom the relationship accounted for only 11.6% of the observed variance ($F_{1,61}$=8.066, p=0.006).

There was a significant difference among activity scores observed at different times of the day ($F_{2,5}$=6.38, p=0.04). Scheffé post-hoc comparisons indicated that activity was significantly lower at noon than those recorded in the morning and in the afternoon.

Discussion:

Statistical Relationships to Activity:

Activity levels were significantly related to EA in all seals except the female. Contrary to reports by Renouf & Noseworthy (1990), there was no significant relationship in the current study between GE and activity except in male #3. The difference between the two results may be attributable to the fact that Renouf & Noseworthy measured activity as social interactions rather than locomotion. Activity levels were fairly uniform during the winter and spring, and the strength of the relationship between activity and EA exhibited by males #1-4 derived from the strong correlation during the breeding and moult periods.

In most animals poor body condition activates a feeding response (and increases activity levels) as a mechanism for maintaining a set body mass or condition (Stanier *et al.* 1984; Steffens & Strubbe 1987). However, it has been proposed that body condition set-points are lowered during predictable periods of low food availability, suppressing the foraging response and leading to low levels of activity (Mrosovsky & Sherry 1980; Sherry 1981). This was evident during the moult when the seals spent a large amount of time hauled out of the water, and ate little despite unrestricted access to food (Chapter 5). This decrease in activity is also seen in wild harbour seals during the moult when thermoregulatory concerns restrict foraging time (Sullivan 1980; Pitcher & McAllister 1981; Härkönen 1987a; Thompson & Rothery 1987; Watts 1992). The suppression of the foraging response during the moult is similar to that exhibited by northern mammals during hibernation (Hudson 1973; Mrosovsky 1990). The effectiveness of hibernation as a means of energy conservation does not derive solely from the energy saved by lowering basal metabolism, but by precluding the animal searching for a non-existent food supply (Lyman 1982).

The seals in the present study exhibited a dramatic increase in activity and decrease in GE during the reproductive season, similar to that reported for male harbour seals in the wild (Sullivan 1981; 1982; Thompson 1988; Thompson *et al.* 1989; Perry 1993). The high levels of activity exhibited by the seals in the current study during the breeding period were supported by utilization of lipid reserves, resulting in increased EA despite a drop in GE.

Hypophagia during the breeding period is typical of many male mammals, even though it occurs at a time of year when activity levels and other energy expenditures are greatest. It is unclear whether hypophagia is a result of time budget constraints, hormonal changes (McMillan *et al.* 1980), opiate antagonists(Plotka *et al.* 1985), or rheostasis (Sherry 1981; Mrosovsky 1990). It is interesting that the captive harbour seals did not avail of the opportunity to feed, exhibiting the same trend of increasing activity and decreasing body condition as their wild counterparts. This suggests that the body condition set-point was lowered during the breeding season, suppressing the foraging response so that the seals were not motivated by hunger during these times.

Unlike the males, the elevated levels of EA exhibited by the female during the reproductive season were not related to high levels of activity. For female seals, the greatest reproductive cost is associated with lactation (Bonner 1984; Oftedal *et al.* 1987; Bowen *et al.* 1992). The female's activity levels decreased during the lactation period, possibly as a mechanism to conserve energy reserves and/or to facilitate contact with their pups (Lawson 1983; Renouf *et al.* 1983; Rosen & Renouf 1993), and only increased during the mating phase, after the pup was weaned and prior to the moult. A similar pattern of behaviour has been reported for wild female harbour seals (Thompson *et al.* 1994).

There was a relationship between EA and activity scores for male #5, although this was due to ontogenetic rather than seasonal variation. As the pup grew older, both EA and activity levels increased. The drop in activity seen during the 1992 breeding season was likely the result of being excluded from the main tank by the older males. Coincident with the drop in activity, male #1 was observed to grab male #5 in his mouth, shake him several times, and toss him out of the main tank; for the rest of the breeding season male #5 remained predominantly on a distant portion of the deck.

During the breeding season there was a deterioration in body condition for both the males and the female brought about by increased energy expenditure and decreased GE (Chapter 4). Although poor condition is often regarded as a negative characteristic, the combination of increased energy output and decreased intake may serve to increase reproductive fitness. For females the presence of a pup precludes anything other than opportunistic feeding (except towards the end of the lactation period; Boness *et al.* 1994), as haul out time and position often affect pup survival. It is also possible that the female's continued presence in the breeding area increases her reproductive success through inciting increased intrasexual competition among the males. For the males, reproductive success is linked to continued presence at the breeding site, via intrasexual competition. For both males and females, lowering the body condition set-point will preclude the normal foraging response, and allow them to undertake energetically expensive breeding behaviour despite declining body condition.

Energetic Cost of Activity:

This chapter examined the statistical relationship between locomotor activity and EA by estimating the proportion of variation observed in the latter accounted for by changes in the former. While it was not possible to determine the energetic cost of activity in relation to EA, the level of activity needed to account for all of the observed EA can be estimated.

The energetic cost of locomotor activity is difficult to ascertain, as activity can affect energy budgets through several avenues, including direct metabolic costs and changes in thermoregulation. Additional difficulties are presented when studying marine mammals, given their divergent physiological responses to diving and surface swimming. There are two general methods for determining the daily cost of activity in marine mammals. Field estimates measure total energy consumption and the cost of activity is calculated as the difference between total consumption and basal metabolism (Costa & Gentry 1986; Costa 1988; Costa *et al.* 1989; Sakamoto *et al.* 1989). Another method combines time budgets with laboratory measures of energy consumption in specific activities to estimate total activity costs (Krockenberger & Bryden 1993; Olesiuk 1993).

A number of studies have specifically examined the relationship between swimming speed and energy expenditure in marine mammals, generally estimating the cost at 2 J x g^{-1} x km^{-1} (Schmidt-Nielsen 1972; Lavigne *et al.* 1982; Innes 1984). This relationship is probably non-linear due to increasing drag forces with increasing velocity and size (Peters 1983), and is also dependent upon body composition and shape (Feldkamp 1987; Fish 1992). More specific estimates have been empirically derived for harbour seals. Davis *et al.* (1985) reported a curvilinear increase in metabolism with swimming speed in adult and juvenile harbour seals. At a speed of 1.4 m/s metabolism was 3.0 times the resting rate for the yearling seals and 2.1 times the resting rate for the adult. Markussen *et al.* (1992b) found that this relationship was linear, although they only tested seals at speeds up to 0.6 m/s. Results from their study predicted that a doubling and tripling of metabolism occurred at 0.8

and 1.5 m/s, respectively, for fed seals, and 0.6 and 1.3 m/s for seals under forced starvation. In comparison, Castellini *et al.* (1985) and Feldkamp (1987) reported that metabolism doubled for adult grey seals and juvenile California sea lions swimming at 1.25 m/s and 1.63 m/s, respectively.

Increased locomotor activity in the water does not always result in increased energy consumption, as diving behaviour and surface swimming can have opposite effects upon metabolism. During deep dives heart rates and core temperatures may be depressed and circulation reduced to peripheral tissues (Scholander *et al.* 1942; Scholander 1964; Kooyman *et al.* 1981; Hindell *et al.* 1992; although see Gallivan & Ronald 1981), adaptations for extending aerobic dive limits (Schusterman 1981; Castellini *et al.* 1985; Kooyman 1985; Cherepanova *et al.* 1993; Thompson & Fedak 1993). It has been noted that several phocid species (e.g., northern eleohant and harp seals) exhibit diving behaviour during what is assumed to be their non-foraging migration phase. It has been suggested that this increased dive time can decrease metabolic costs to the point where overall energy expenditure is decreased even though the total distance traveled is greater.

Although locomotor activity such as swimming has a direct energetic cost, the overall effect may be to decrease energy expenditure by avoiding hyperthermia. As heat dissipation from a submerged mammal is about 25 times greater than in air (Ridgway 1972), swimming in water below a critical temperature will result in a loss of heat, despite the extra energy generated by swimming. This will reduce overall energy expenditure by serving as a behavioural thermoregulatory response when the seal is under heat stress (Gentry 1973; Whittow *et al.* 1975; Whittow 1987; Watts 1992). Increases in peripheral circulation will promote the dissipation of large quantities of heat (Scholander *et al.* 1950c; Bartholomew & Wilke 1956; Brodie 1975), facilitated by increases in flipper surface temperatures during swimming (Davydov & Marakova 1965; Iversen & Krog 1973; McGinnis 1975).

Statistically, activity levels in the present study accounted for up to 69% of the variance observed in EA. Although it was not possible to quantify the amount of EA attributable to activity, it is possible to estimate the level of activity needed to account for all of the EA. Among the adult seals in this study, EA reached a maximum of 35-40 MJ/d during the breeding season. At this time of year expenditures due to basal metabolism accounted for approximately 8.5 MJ/d (assuming basal metabolism was equal to predictions by Kleiber 1975, and an average mass of 90 kg). Therefore, to fully account for EA, the cost of activity would have to be three times that of basal metabolism (i.e., a 300% increase in total metabolism). According to data from Davis *et al.* (1985) this suggests that the seals would have to continuously surface swim at a speed of 1.9 m/s. Similar calculations were performed by Underwood (1971) for Arctic fox, with the same unlikely results. As Prestrud (1991) noted for that study, only an unreasonable level of locomotor activity would account for the observed seasonal changes in energy utilization. For the seals in the present study, it is likely that changes in locomotor activity contributed to changes in EA. However, it is also evident that other bioenergetic expenditures (including other forms of activity such as social interactions) must contribute to seasonal variation in EA.

Summary:

- There was a positive relationship between locomotor activity scores and available energy (EA) in the adult male seals;
- the strength of this relationship was derived largely from high levels of EA and activity during the breeding period, and low levels during the moult;
- although the energetic cost of activity was not quantified, it does not appear feasible that locomotor activity alone could account for the high levels of EA exhibited during the breeding season by the adult males; and
- there was no significant relationship between activity scores and EA for the female, largely because of low levels of activity and high EA during the breeding period.

Chapter 10 - Seasonal Changes in Condition

Introduction:

The external blubber layer of marine mammals serves in adjusting buoyancy, streamlining the body, maintaining thermoregulation, and as an energy reserve. As demonstrated in Chapter 4, the blubber layer undergoes substantial seasonal variation in both absolute mass and in relation to core body mass, at least partially influenced by reproductive cycles (Rice & Wolman 1971; Fedak & Anderson 1987). However, at times the multiple functions of this layer may be in conflict. It has been suggested that the distribution of blubber across the body represents a compromise between these competing factors (Pond & Ramsay 1992). As a corollary, species under similar selective pressures should present comparable patterns in the distribution and seasonal changes in their blubber layer.

This chapter examines changes in blubber distribution in the seals throughout the year. Previous studies have documented seasonal variation in blubber depth in harbour seals (Bishop 1967; Bigg 1969; Boulva & McLaren 1979; Pitcher 1986; Baird & Stacey 1989; Renouf & Noseworthy 1991), but were either descriptive or examined changes in blubber depth at only a single location, the xiphoid process of the sternum.

In contrast, Ryg *et al*. (1988) and Slip *et al*. (1992) examined seasonal changes in blubber distribution and body shape at several sites along the trunk of ringed and southern elephant seals, respectively. Ryg *et al*. (1988) found that ringed seals preferentially lost blubber at several sites during the period of weight loss, while Slip *et al*. (1992) reported that elephant seals lost blubber at similar rates over all areas of the body.

Variation in the distribution of blubber is energetically important as changes in its insulative capability affect thermoregulatory costs. Most studies which have examined the thermoregulatory characteristics of the blubber layer of seals have treated it as an insulating plane covering a heat-producing surface (Watts *et al.* 1993). However, Ryg *et al.* (1988) and later Hokkanen (1990) noted that heat loss from a cylindrical body (such as a phocid body) does not depend upon the thickness of the blubber layer, but rather on the ratio between blubber depth and the radius of the body. Ryg *et al.* (1988) proposed that this parameter, termed the 'd/r ratio', should exhibit less seasonal change than blubber depth alone. Similarly, seals should show less variation along their body in this ratio than in blubber depth, particularly during those periods when fat reserves are minimal.

This chapter examines seasonal changes in blubber depth, girths, d/r ratios, and blubber distribution over a two year period, and how these variables differed across the body. It also tests two hypotheses: 1) d/r ratios are more constant along the trunk and exhibit less seasonal variation than blubber depth, and 2) blubber is preferentially lost from 'over-insulated' areas of the trunk.

Method:

Four morphological measures were examined: blubber depth, girth, d/r ratio, and Intergirth Fat Volume (IFV). These measures were taken in reference to six sites along the axis of the seal, numbered anterior to posterior (Chapter 2, Figure 2). Girth estimates were taken directly from weekly morphological measures, while blubber depth was calculated as the average of weekly dorsal and lateral blubber depth estimates (except at site #1, where only dorsal blubber depth was obtained). The d/r ratios were calculated as the quotient of interpolated body radius to averaged blubber depth (Ryg *et al.* 1988), where body radius was estimated as girth/2π (Ryg *et al.* 1988). The five IFVs represented the blubber volumes between the six standard sample sites, as estimated by the truncated cone model modified from Gales & Burton (1987; Chapter 4; Appendix B).

To test for overall circannual changes, the data were partitioned into Winter/Spring (January 1- June 31) and Summer/Fall periods (July 1 - December 31), pooling data from

1992 and 1993. This loosely divided the data into periods of 'good' (high blubber mass) and 'poor' (low blubber mass) condition. The July 1 division represents the middle of the breeding and pupping season in this group of seals.

To determine whether there were significant seasonal differences at each of the sample sites for each morphological measure, separate mixed factorial design ANOVAs were used for each group of morphological measurements (girth, blubber depth, IFV, and d/r ratio) for data from each of the seals. In cases with significant (site x period) interactions, an analysis of the simple main effects was used (Keppel & Zedeck 1989) to assess specific trends.

To test whether there were significant differences among sample sites for each morphological measure, within each season, single factor ANOVAs were used with the data from each seal. Scheffé post-hoc comparisons were used to further test for significant differences between particular sites.

To determine whether seasonal changes in d/r ratios were less than seasonal changes in blubber depth, the degree of circannual change in d/r ratios and blubber depth was calculated as the ratio of maximum yearly change to maximum value (i.e., [max-min]/max) for each variable at each site. Separate ratios for 1992 and 1993 were calculated for each seal. Data from male #5 were not used in this or the following analysis, as changes in the data reflected net annual growth rather than seasonal variation. This produced 12 values of relative change in both d/r ratios and blubber depth, which were compared by a paired t-test. For illustrative purposes, averages of the individual mean changes of d/r ratios, blubber depth, and IFVs at the six sample sites were calculated for the adult males (males #1-4), and all adult seals (males #1-4 and female).

To test whether d/r ratios were more constant along the seals' axis than blubber depth, weekly d/r ratios and blubber depths along the axis were expressed as a ratio of the weekly mean. Weekly variance of relative d/r ratios and blubber depths were then compared by a paired t-test to determine whether there was greater overall variation in d/r ratios or blubber depth along the axis of the seal.

Results:

Significant seasonal differences were found for most of the morphological measurements (Table 28). All seals exhibited significant seasonal differences in IFVs at all intervals (Figure 31, Table 29), with the exception of male #5 who displayed no significant differences at any sites.

There was a significant seasonal difference in girth at sites #2, 3, 4, and 5 for all seals (Figure 32, Table 30). There was a significant difference in girth at site #1 for male #5 only, and at site #6 in all seals except male #4 and the female.

Similar results were found for both the combined blubber depths (Figure 33, Table 31) and the d/r ratios (Figure 34 Table 32). Significant seasonal differences were found for both measurements at sites #2, 4, and 5 for all seals, and at site #3 in all seals except for male #2. Differences were found at site #6 for all seals except in male #4 and the female. No differences were found at site #1 in any of the seals.

For all the adult seals, there was greater variation in blubber depth among the six measurement sites than for d/r ratios (Table 33). Circannual variation in blubber depth was greater than for d/r ratios in all seals (Table 34). Averaged across all adult seals, annual decreases in the d/r ratio were less than those for blubber depth at all sample sites, except for the head region. Seasonal changes in blubber depth were greatest in the neck region (site #2), decreasing slightly towards the tail (Figure 35); changes in the d/r ratio followed a similar pattern. The relative decreases in IFVs were greatest in the middle sections (>50%) and slightly lower in the anterior and posterior regions (approx. 45%).

Table 28:

Seasonal differences in morphological measurements. The data from 1992 and 1993 were divided into Winter/Spring (01 Jan - 30 June) and Summer/Fall (01 July - 31 December) periods. The numbers represent the sample points for morphological measures along the axis of the seal (1-6, anterior to posterior), except for the IFVs where the numbers refer to the anterior site bounding the IFV. Seasonal differences, as tested using an analysis of simple main effects from mixed-factorial ANOVAs, were regarded as significant (designated by '√'; nonsignificant results marked by '•') at $p \leq 0.01$ (modified for the number of comparisons).

	Girth						IFV					Blubber Depth						d′r Ratio					
Subject	1	2	3	4	5	6	1	2	3	4	5	1	2	3	4	5	6	1	2	3	4	5	6
Male 1	•	√	√	√	√	√	√	√	√	√	√	•	√	√	√	√	√	•	√	√	√	√	√
Male 2	•	√	√	√	√	√	√	√	√	√	√	•	√	•	√	√	√	•	√	•	√	√	√
Female	•	√	√	√	√	•	•	√	√	√	√	•	√	√	√	√	•	•	√	√	√	√	•
Male 3	•	√	√	√	√	√	√	√	√	√	√	•	√	√	√	√	√	•	√	√	√	√	√
Male 4	•	√	√	√	√	•	√	√	√	√	√	•	√	√	√	√	•	•	√	√	√	√	•
Male 5	√	√	•	•	√	√	•	•	•	•	•	•	√	√	√	√	√	•	√	√	√	√	√

Figure 31:

Estimates of Intergirth Fat Volume (cm^3) for the Winter/Spring (circles) and Summer/Fall (squares) periods. The values are marked midway between the six standard sites from which they were calculated. Significant differences are marked.

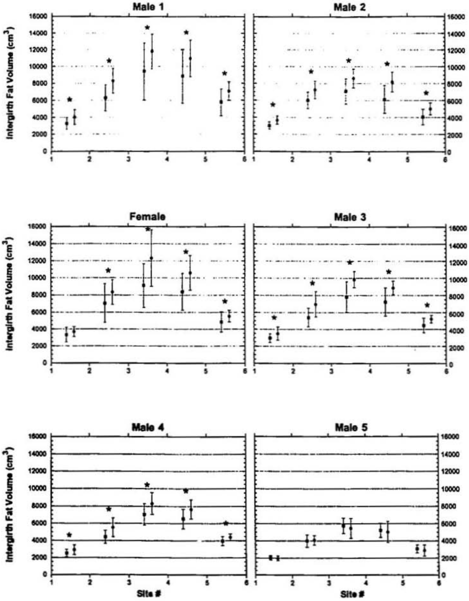

Male 1
Male 2
Female
Male 3
Male 4
Male 5
Intergirth Fat Volume (cm^3)
Intergirth Fat Volume (cm^3)
Intergirth Fat Volume (cm^3)
0
2000
4000
6000
8000
10000
12000
14000
16000
1
2
3
4
5
6
Site #
Site #
*

Table 29:

Differences in Intergirth Fat Volumes along the axis. Interval Fat Volumes (IFVs) were estimated using the truncated cone method from Gales & Burton (1987) (see text for details). The data from 1992 and 1993 were divided into Winter/Spring and Summer/Fall periods. The numbers represent the anterior most girth bounding the IFV (1-6, anterior to posterior). They are arranged from least to greatest mean calculated independently for each seal for each period. Underlined values indicate non-significant differences (p>.01) as determined by Scheffé post-hoc pairwise comparisons. Results of the overall ANOVA (F-value and degrees of freedom) are also given. In all cases the ANOVAs were significant at p<.0001.

Subject	Season	d.f.	F-Value	Differences
Male 1	Winter/Spring	4,190	144.0	1 5 2 4 3
Male 1	Summer/Fall	4,220	51.8	1 5 2 4 3
Male 2	Winter/Spring	4,190	199.8	1 5 2 4 3
Male 2	Summer/Fall	4,220	92.7	1 5 2 4 3
Female	Winter/Spring	4,190	135.4	1 5 2 4 3
Female	Summer/Fall	4,220	72.1	1 5 2 4 3
Male 3	Winter/Spring	4,190	295.6	1 5 2 4 3
Male 3	Summer/Fall	4,220	110.6	1 5 2 4 3
Male 4	Winter/Spring	4,185	211.3	1 5 2 4 3
Male 4	Summer/Fall	4,220	201.2	1 5 2 4 3
Male 5	Winter/Spring	4,185	114.2	1 5 2 4 3
Male 5	Summer/Fall	4,215	226.8	1 5 2 4 3

Figure 32:

Girth measurements (cm) for the Winter/Spring (circles) and Summer/Fall (squares) periods. Seasonal means ± 1 S.D. at the six standard sites are given. Significant differences are marked with an asterix.

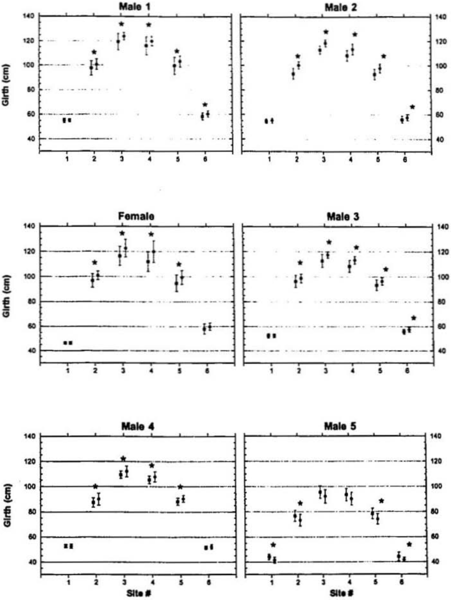

Male 1
Male 2
Female
Male 3
Male 4
Male 5
Girth (cm)
Site #
140
120
100
80
60
40
1
2
3
4
5
6
★

Table 30:

Differences in girth along the axis. The data from 1992 and 1993 were divided into Winter/Spring and Summer/Fall periods. The sample sites (1-6, anterior to posterior) are arranged from least to greatest mean. Underlined values indicate non-significant differences (p>.01). Results of the ANOVA testing for overall differences are also given. In all cases the ANOVAs were significant at p<.0001.

Subject	Season	d.f.	F-Value	Differences
Male 1	Winter/Spring	5,240	3047.3	1 6 2 5 4 3
Male 1	Summer/Fall	5,264	1074.1	1 6 2 5 4 3
Male 2	Winter/Spring	5,240	3160.0	1 6 5 2 4 3
Male 2	Summer/Fall	5,264	2230.1	1 6 5 2 4 3
Female	Winter/Spring	5,240	1403.7	1 6 5 2 4 3
Female	Summer/Fall	5,264	1071.6	1 6 5 2 4 3
Male 3	Winter/Spring	5,240	4577.6	1 6 5 2 4 3
Male 3	Summer/Fall	5,264	1924.7	1 6 5 2 4 3
Male 4	Winter/Spring	5,234	2396.7	6 1 2 5 4 3
Male 4	Summer/Fall	5,264	4042.3	6 1 2 5 4 3
Male 5	Winter/Spring	5,240	1238.9	1 6 2 5 4 3
Male 5	Summer/Fall	5,264	1451.3	1 6 2 5 4 3

Figure 33:

Mean blubber depth (mm) for the Winter/Spring (circles) and Summer/Fall (squares) periods. Blubber depth was calculated as the mean of dorsal and lateral measurements, except for site #1 where only a dorsal measurement was taken. Seasonal means ± 1 S.D. at the six standard sites are given. Significant differences are marked with an asterix.

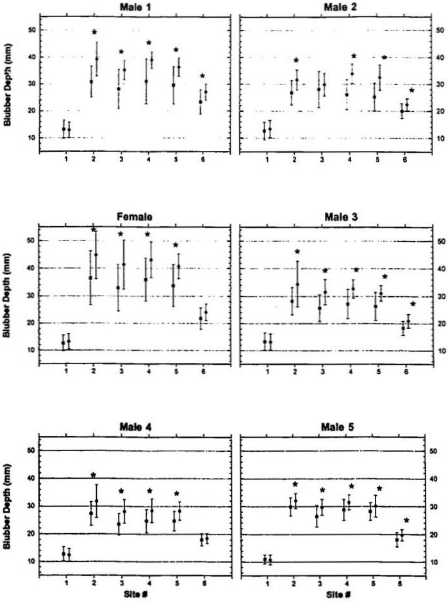

Male 1
Male 2
Female
Male 3
Male 4
Male 5
Blubber Depth (mm)
10
20
30
40
50
*
1
2
3
4
5
6
Site #

Table 31:

Differences in average blubber depth along the axis. Average blubber depth was calculated as mean of dorsal and lateral depth estimates except for site 1 where only a dorsal estimate was used. The data from 1992 and 1993 were divided into Winter/Spring and Summer/Fall periods. The sample sites (1-6, anterior to posterior) are arranged from least to greatest mean. Underlined values indicate non-significant differences ($p>.01$). Results of the ANOVA testing for overall differences are also given. In all cases the ANOVAs were significant at $p<.0001$.

Subject	Season	d.f.	F-Value	Differences
Male 1	Winter/Spring	5,228	263.1	$1\ 6\ \underline{\underline{3\ 5}\ 4\ 2}$
Male 1	Summer/Fall	5,264	53.3	$1\ 6\ \underline{3\ 5\ 2\ 4}$
Male 2	Winter/Spring	5,228	179.3	$1\ 6\ \underline{3\ \underline{2\ 5}\ 4}$
Male 2	Summer/Fall	5,264	65.8	$1\ 6\ \underline{5\ 4\ 2\ 3}$
Female	Winter/Spring	5,228	166.5	$1\ 6\ \underline{5\ 3\ 4\ 2}$
Female	Summer/Fall	5,264	80.2	$1\ 6\ \underline{3\ 5\ 4\ 2}$
Male 3	Winter/Spring	5,228	132.9	$1\ 6\ \underline{5\ 3\ 4\ 2}$
Male 3	Summer/Fall	5,264	80.5	$1\ 6\ \underline{3\ 5\ 4\ 2}$
Male 4	Winter/Spring	5,222	137.2	$1\ 6\ \underline{3\ 5\ 4}\ 2$
Male 4	Summer/Fall	5,264	104.7	$1\ 6\ \underline{3\ 5\ 4}\ 2$
Male 5	Winter/Spring	5,222	363.3	$1\ 6\ \underline{3\ \underline{5\ 4}\ 2}$
Male 5	Summer/Fall	5,258	249.7	$1\ 6\ \underline{3\ \underline{5\ 4}\ 2}$

Figure 34:

Estimates of the blubber depth to body radius ratio (d/r ratio) for the Winter/Spring (circles) and Summer/Fall (squares) periods. Seasonal means ± 1 S.D. at the six standard sites are given. Significant differences are marked with an asterix.

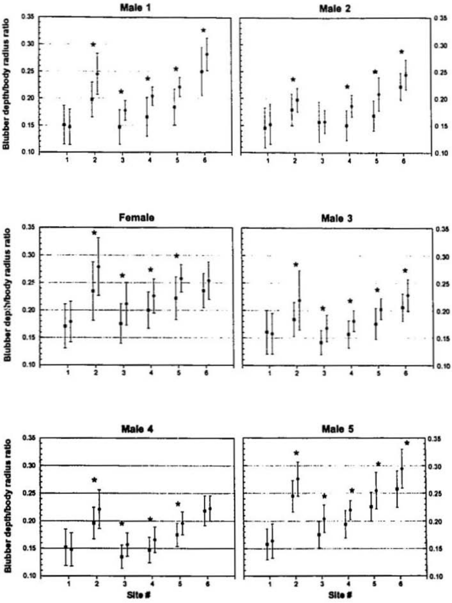

Male 1
Male 2
Female
Male 3
Male 4
Male 5
Blubber depth/body radius ratio
0.10
0.15
0.20
0.25
0.30
0.35
1
2
3
4
5
6
Site #
*

Table 32:

Differences in d/r ratios along the axis. The d/r ratio was calculated as the ratio of average fat depth to body radius. The data from 1992 and 1993 were divided into Winter/Spring and Summer/Fall periods. The sample sites (1-6, anterior to posterior) are arranged from least to greatest mean. Underlined values indicate non-significant differences (p>.01). Results of the ANOVA testing for overall differences are also given. In all cases the ANOVAs were significant at p<.0001.

Subject	Season	d.f.	F-Value	Differences
Male 1	Winter/Spring	5,228	121.8	1 3 4 5 2 6
Male 1	Summer/Fall	5,264	51.2	3 1 4 5 2 6
Male 2	Winter/Spring	5,228	62.2	1 3 4 2 5 6
Male 2	Summer/Fall	5,264	37.8	1 4 3 5 2 6
Female	Winter/Spring	5,228	37.7	1 3 4 6 5 2
Female	Summer/Fall	5,264	23.4	1 3 4 5 2 6
Male 3	Winter/Spring	5,228	29.0	1 3 4 5 2 6
Male 3	Summer/Fall	5,264	27.1	3 4 1 5 2 6
Male 4	Winter/Spring	5,222	59.6	1 3 4 5 2 6
Male 4	Summer/Fall	5,264	68.8	3 4 1 5 2 6
Male 5	Winter/Spring	5,222	104.0	1 3 4 5 2 6
Male 5	Summer/Fall	5,258	93.8	1 3 4 5 2 6

Table 33:

Comparison of variance in d/r ratios and blubber depth. Weekly variance along the axis of the seal (male #5 excluded) in each of the morphological measures was calculated as the variance of raw scores for the six sample sites expressed as a ratio of mean weekly score. The weekly variance in d/r ratios and blubber depth were compared by a paired one-tailed t-test. Significant results indicate that blubber depth displayed significantly greater variation along the axis of the seals than d/r ratios. Comparison were made across the entire year, and within the Winter/Spring and Summer/Fall periods.

	Period		
Seal	Winter/Spring	Summer/Fall	Overall
Male 1	$t_{38} = 10.090$	$t_{44} = 2.174$	$t_{83} = 6.494$
	$p < .0001$	$p = .0351$	$p < .0001$
Male 2	$t_{38} = 8.856$	$t_{44} = 6.756$	$t_{83} = 10.828$
	$p < .0001$	$p < .0001$	$p < .0001$
Female	$t_{38} = 30.540$	$t_{44} = 12.624$	$t_{83} = 22.884$
	$p < .0001$	$p < .0001$	$p < .0001$
Male 3	$t_{38} = 13.525$	$t_{44} = 6.699$	$t_{83} = 12.545$
	$p < .0001$	$p < .0001$	$p < .0001$
Male 4	$t_{37} = 10.419$	$t_{44} = 4.739$	$t_{82} = 9.454$
	$p < .0001$	$p < .0001$	$p < .0001$

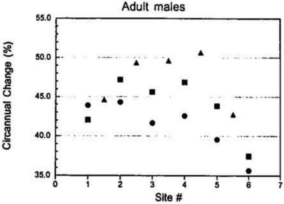
Table 34:

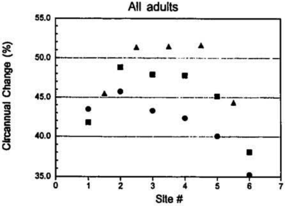
Circannual change in d/r ratios and blubber depth. Circannual change was calculated as the ratio of maximum yearly change to maximum value (i.e., [max-min]/max) for each parameter at each site. Separate ratios for 1992 and 1993 were calculated for each seal (male #5 excluded). This produced 12 values of relative change in both d/r ratios and blubber depth, which were compared by a paired t-test (t-values at 11 d.f. and probability values are given).

Seal	Δ Blubber	Δ d/r ratio	t- value	p-value
Male 1	.552	.513	3.023	.0083
Male 2	.531	.506	3.562	.0045
Female	.553	.500	4.905	.0005
Male 3	.482	.455	3.114	.0099
Male 4	.553	.532	2.413	.0345

Figure 35:

Change in mean blubber depth (squares), blubber depth/radius ratio (d/r ratio; circles), and Intergirth Fat Volume (IFV; triangles) during the year. Annual change was calculated as the ratio of annual range to maximum value multiplied by 100. Data for the top figure is from males #1-4, while the bottom figure is derived from data for males #1-4 and the female. Results for blubber depth and d/r ratios are given at the six standard sites, while those for IFVs are given midway between the relevant sites.


Adult males
Circannual Change (%)
55.0
50.0
45.0
40.0
35.0
0
1
2
3
4
5
6
7
Site #


All adults
Circannual Change (%)
55.0
50.0
45.0
40.0
35.0
0
1
2
3
4
5
6
7
Site #

Discussion:

It has often been assumed that seals will preferentially lose blubber over muscle mass, as the energetic yield from the latter is far less than from the former (Chapter 4). However, it has also been proposed that, under certain conditions, thermoregulatory considerations may dictate that core mass will also be depleted (Stewart & Lavigne 1980; Worthy & Lavigne 1983a; Øritsland *et al.* 1985).

Ryg *et al.* (1988) hypothesized that core mass was lost in order to maintain a constant d/r ratio and, therefore, constant insulative effectiveness. This led to their prediction that this ratio should change less than blubber depth during the year. The results of this study are consistent with those found by Ryg and co-workers for ringed seals, although large circannual changes were still evident in the d/r ratios of the harbour seals. In all cases (except for the poorly insulated head region), seasonal changes in the d/r ratios were less than changes in either blubber depth or volume, similar to the results reported by Slip *et al.* (1992) for southern elephant seals. Both of these studies support Ryg *et al.*'s suggestion that seals should lose mass in a way that maximizes insulative effectiveness.

Ryg *et al.* (1988) also suggested that certain portions of the body were 'over-insulated' (i.e., those that had the highest d/r ratios), and that these should be the sites of greatest blubber loss. In ringed seals, they found the highest d/r ratios towards the end of the seals (70-80% of the standard body length posterior to the snout), and that these sites also showed the greatest percent seasonal decrease.

In the harbour seals, the greatest d/r ratios were towards the posterior of the body (site #6). Yet, contrary to predictions by Ryg *et al.* (1988), this site showed the smallest relative seasonal change. This might be expected as the high d/r ratio was the result of a small radius (the 'hips' of the animal). Despite the high d/r ratio, absolute blubber depth at this site was low throughout the year, and was probably limited in how far it could be depleted. The neck region (site #2) had a high d/r ratio resulting from a high blubber depth, and this area exhibited the greatest seasonal change of any of the sites. This result would tend to support Ryg *et al.*'s (1988) suggestion that blubber is preferentially lost from 'over-insulated' areas.

Contrary to the results of Ryg *et al.* (1988) and the present study, Slip *et al.* (1992) found that d/r ratios were fairly uniform along the axis of southern elephant seals, and that blubber was lost equally along the length of the body. Part of the discrepancy between these results may be explained by the duration and time of the various studies and, subsequently, the relative condition of the seals. Although the studies by Ryg *et al.* (1988) and Slip *et al.* (1992) were both short-term, the former examined changes between April and June, encompassing both the breeding and moult periods, while the latter measured differences during the moulting fast; the current study examined changes over the entire year. Ryg *et al.*'s hypothesis assumes that the seals have 'excess' blubber reserves at the start of the study. Although elephant seals were not in 'poor' condition at the start of the moult, their reserves were already reduced compared to the onset of the breeding season. They therefore lacked the extensive 'over-insulated' areas from which to draw, so that blubber was depleted more equally along the body than for ringed or harbour seals.

Alternately, the difference may be related to differences in high and low latitude strategies. Species at higher latitudes would be expected to favour a lipid loading strategy in response to more seasonal food supplies. Although elephant seals inhabit low latitudes for part of the year, ringed seals are primarily polar through the entire year and would be expected to accumulate greater energy reserves. This is supported by evidence that ringed seals end their breeding and moulting periods with substantial blubber stores despite minimal core tissue loss (Ryg *et al.* 1990). This would suggest that ringed seals begin the breeding season with more extensive 'over-insulation', which would be preferentially lost during periods of negative energy balance.

Finally, it should be noted that most of the theories addressing core versus blubber loss make the assumption that the seals are trying to minimize heat loss (Stewart & Lavigne

1980; Worthy & Lavigne 1983a; Øritsland *et al.* 1985; Ryg *et al.* 1988). While this may be true of polar species (particularly for young pups), it may not be universally applicable. It would seem likely that maximizing heat dissipation would be a greater concern for more tropical (e.g. monk seals, *Monachus* spp.) and temperate species during the summer months (Watts 1992) and, therefore, would affect the manner in which body composition and blubber distribution changes during the year.

Summary:

- Harbour seals underwent significant changes in blubber distribution and body morphology during the year;
- the greatest seasonal changes took place in the neck region, one of the more heavily insulated areas of the body;
- the ratio of insulation thickness to body diameter (d/r ratio) exhibited less seasonal change than blubber depth alone, perhaps an adaptation to maintaining insulative properties; and
- the d/r ratio was more constant along the axis than blubber depth itself, suggesting that blubber was distributed to maximize its insulative effectiveness.

Chapter 11 - Conclusions

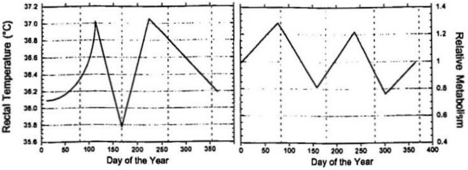
This study documents circannual variation in several components of the energy budgets of captive harbour seals. Accurate estimates of the extent and pattern of seasonal variation in the elements of energy budgets are important for two reasons. First, examining concurrent changes in these parameters leads to a better understanding of their interaction and adaptive significance. Second, documenting seasonal changes in these variables allows for more accurate estimates of their bioenergetic value and effect, of particular importance in the construction of population energetics models.

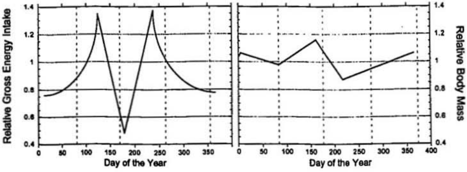
Specifically, this study had four objectives: 1) integrate changes in body mass and gross energy intake (GE) to quantify circannual changes in available energy (EA); 2) document seasonal variation in metabolism, rectal temperature, and locomotor activity; 3) test whether the observed variation in metabolism, rectal temperature, and locomotor activity were statistically related to changes in EA; and 4) determine the extent to which the observed circannual variation in these three parameters accounted for the observed energetic changes in available energy.

Significant seasonal variation was found in all of the components of the seals' energy budgets examined in the current study. The relationship between these variables is difficult to discern, as the changes did not follow a uniform function (Figure 36). As predicted, changes in body mass throughout the year were not directly proportional to changes in gross energy intake. A cursory examination of these data suggests that the seals demonstrated alternating periods of high energy conservation and utilization. While changes in both of these variables have been documented previously in harbour seals, few studies have examined them simultaneously, and none have attempted to integrate these changes to determine their energetic effect (i.e., on available energy). The magnitude of changes found in this study were greater than originally anticipated: concurrent changes in body mass and

Figure 36:

Changes in relative body mass, gross energy intake, mass-specific metabolism as well as rectal temperature with day of the year. The lines represent the formulae presented in Tables 2, 9, 19 and 23, respectively. The overall significance of the lines are presented in Table 35.


Rectal Temperature (°C)
37.2
37.0
36.8
36.6
36.4
36.2
36.0
35.8
35.6
0
50
100
150
200
250
300
350
Day of the Year
Relative Metabolism
1.4
1.2
1
0.8
0.6
0.4
0
50
100
150
200
250
300
350
400
Day of the Year


Relative Gross Energy Intake
1.4
1.2
1
0.8
0.6
0.4
0
50
100
150
200
250
300
350
Day of the Year
Relative Body Mass
1.4
1.2
1
0.8
0.6
0.4
0
50
100
150
200
250
300
350
400
Day of the Year

GE resulted in a range in EA of 50-350 MJ/week. This variation suggests that a seven-fold shift occurs in the energy demands of other components of the energy budget (singly or in combination) throughout the year.

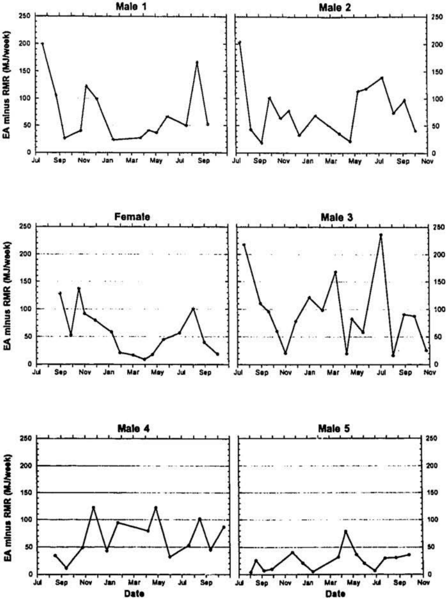
It was proposed that the observed variation in EA could be accounted for by changes in metabolism, activity, and/or rectal temperature. In accordance with initial predictions, substantial changes in RMR (45-129 MJ/week) occurred throughout the year. However, contrary to expectations, these changes were minor compared with the estimated changes in EA. Concurrent circannual variation in EA and RMR meant that, while almost all of EA was attributable to RMR during certain times of the year (e.g., the winter), EA exceeded RMR requirements by up to 200 MJ/week at other times (primarily during the breeding period and after the moult; Figure 37).

Activity levels were also proposed as a source of variation in EA. Behavioural observations suggest that the activity levels of harbour seals are highly variable. At certain times of the year they appear to spend the majority of their time hauled out, while during the breeding season mature males are highly active in intra- and intersexual interactions. Locomotor activity scores were statistically related to EA in all of the seals except the female. The strength of the relationship in the mature males was derived largely from the high levels of activity and EA during the breeding season (consistent with the high reproductive effort documented in wild male harbour seals). It seems likely that, for the adult males, a large proportion of EA was devoted to activity during this period.

Although the cost of locomotor activity was not quantified, the highest levels of EA (even after removing the cost of RMR) could not be accounted for by the theoretical cost of surface swimming (see Chapter 9). However, social interactions and inter- and intrasexual competition also have energetic costs. Consistent with behavioural pattern observed in the wild, Renouf & Noseworthy (1990) found that social interactions among a group of captive harbour seals were higher after the breeding and moult periods, than during them. These

Figure 37:

Changes in the remainder of available energy (EA) minus resting metabolic rate (RMR). Available energy was calculated as the sum of production and net energy. Data are presented separately for the six seals for the period July 1992 until November 1993.


Male 1
Male 2
Female
Male 3
Male 4
Male 5
EA minus RMR (MJ/week)
250
200
150
100
50
0
Jul
Sep
Nov
Jan
Mar
May
Jul
Sep
Nov
Date

social interactions, in addition to other types of activity, probably accounted for the majority of EA, particularly during the breeding season. Clearly, given the results of this study, additional research is needed into the activity patterns of seals, and the energetic costs of specific activities (e.g., Birt-Friesen *et al.*, 1989).

In contrast to males, the high levels of EA for the female during the mating period were concurrent with low levels of activity. The high levels of EA estimated for the female during the breeding period were likely attributable to the costs of lactation, which is assumed to constitute the highest reproductive cost for female seals (Bonner 1984; Oftedal *et al.* 1987). Bowen *et al.* (1992) estimated that body mass loss in harbour seal females during the first 80% of the lactation period represented an energy expenditure of 714 MJ. Assuming this were true for the captive female, lactation costs would account for a large proportion of the observed EA unaccounted for by RMR.

It is inevitable that some of the observed EA was attributable to components of the bioenergetic system which were not measured in the present study. In Chapter 8, it was proposed that the observed changes in rectal temperatures were the result of changes in the deep body set-point or core-tissue definition, rather than a reflection of insufficient thermoregulation. However, this does not preclude the transfer of thermal energy between the seal and the environment. Heat dumping is a well-documented adaptation to avoid hyperthermia, using the physiological response of vasodilation and/or the behavioural response of entering the water. In such circumstances excess heat from work, digestion, or solar and infrared radiation is removed from the system by convection, conduction and/or evaporation. Unfortunately, the proportion of EA that may have been lost through these processes is beyond the scope of this study.

Mathematical formulae were derived to describe the observed circannual changes in several of the variables, accounting for 30-67% of the observed variance (Table 35). As these are statistically significant values, the use of these formulae will reduce potential bias

Table 35:

The proportion of observed variance (r^2) in relative body mass, relative gross energy intake, relative mass-specific metabolism, and rectal temperature explained by the mathematical formulae relating changes to day of the year. The formulae are given in Tables 2, 9, 19, and 23, respectively, and were originally derived from the combined data of males #1-3. They were also applied to two additional sets of data: males #1-4, and males #1-3 and the female. All formulae were significant at alpha ≤0.01.

	Proportion of Variance Explained		
Variable	Males 1-3	Males 1-4	Males 1-3 and Female
Body Mass	0.67	0.58	0.62
Gross Energy	0.63	0.47	0.51
Metabolism	0.51	0.47	0.46
Rectal Temperature	0.42	0.39	0.30

over predictions using mean annual values. The complex interactions of the energetic components highlight the need to investigate seasonal changes in variables in terms of overall changes in the energy budget.

Although the extent of the observed seasonal variation may not have been predicted, it should not be surprising that some degree of circannual changes occurred. Although pinnipeds are homeotherms, this does not imply that their physiological processes are not subject to periods of fluctuation. Homeothermy implies a controlled response to changing conditions (e.g., rheostasis), not a static state. Animals which live in an environment which undergoes predictable changes (e.g., food availability, temperature) must adapt to those changes in order to maximize reproductive fitness (or suffer the inevitable consequences of natural selection).

Therefore, seals and other homeotherms should not be regarded or studied as static entities. Specifically, the results from short-term studies can not be applied across an entire year or lifetime. Temporal variation needs to be taken into account when measuring physiological processes or behaviour, as the information derived from short-term studies may result in misrepresentative or inaccurate conclusions. For example, estimates of metabolism in adult harbour seals during the late fall averaged approximately 45 MJ/week, while those taken just a few months later were estimated at 130 MJ/week. The possible implications of this difference are enormous if, for example, one were to estimate the annual food consumption of a population of 1,000 adult harbour seals. Many "rough" estimates of prey consumption assume that total energy intake is approximately three times basal metabolism (contrary to the results of the present study). Given this assumption, the differences in estimates of RMR due to sampling only a few months apart would result in a potential error in estimated prey consumption of 4.42 TJ (4.42×10^{13} J), which translates into approximately 5800 metric tons of herring!

The previous example demonstrates the potential impact of short-term sampling, which may lead to inaccurate estimates if they are measured at a time of the year non-representative of annual means. However, not only is it important to obtain accurate mean annual estimates, but incorporation of natural variation is also critical. For example, population energetics models are used primarily to predict the amount of food that an individual or population will consume. The importance of accurate marine mammal bioenergetic models has increased with the public perception that there is significant competition between seals and humans over diminishing fishery resources (e.g., Beddington *et al.* 1985). Most marine mammal bioenergetic models incorporate only net annual changes into their parameters, omitting the possible effects of circannual variation (Härkönen & Heide-Jørgensen 1991; Markussen & Øritsland 1991; Markussen *et al.* 1992a; Lockyer 1993; Olesiuk 1993). Even if the estimates used in the model accurately reflect annual means, failing to incorporate circannual variation will lead to additional errors. Primarily, the consumption of the population is incorrectly assumed to be evenly distributed throughout the year. This is a critical error when the model is attempting to predict the interactions of migratory prey and/or predator species in different oceanographic regions.

Dynamic models are certainly more representative of real systems than static ones, and incorporating seasonal variation into bioenergetic models will further improve their predictive capabilities by decreasing unaccounted-for variation. Yet research resources are limited and decisions must be made regarding which areas warrant further research efforts: those parameters which most affect the overall energy budget (as construed through sensitivity analyses), or those for which the least data exist (and, therefore, for which the accuracy and effects are unknown). For example, the current study demonstrates that variation in GE or body mass has a greater energetic impact than changes in resting metabolism and, therefore, that greater effort should perhaps be expended towards investigating these factors. Conversely, it can be argued that research should be directed towards examining the costs of activity, for which few estimates exist.

Incorporating natural variation of individual energy budget components will doubtless lead to more dynamic models, although it is still unclear whether this will, in fact, lead to greater accuracy, as adequate testing criteria are yet to be formulated. However, it has also been suggested that the entire process of 'fine-tuning' bioenergetic models at the level of the individual might be relatively wasteful. Given that one of the primary purposes of marine mammal bioenergetic models is to estimate prey consumption, it may be argued that the uncertainty in other components of the ecosystem overshadow any refinement at the level of the individual predator (Lavigne 1994; Worthy 1995; Lavigne in press). For example, while the uncertainty in estimated prey consumption by harbour seals in the previous example may seem substantial, it must be viewed within the context of such factors as the uncertainty of current (prey and predator) population size, tempered by our lack of knowledge in interspecific interactions and the functioning of the food web as a whole.

In addition, fine-tuning specific components of energy budgets at the level of the individual may not be the best means to answer specific questions, such as: "How much of each type of fish do seals eat?", a common question in current fisheries management. Rather, various experimental designs have been proposed to answer these questions directly. McLaren & Smith (1985) suggested that "the experimental introduction of harbor seals into well-chosen lakes might tell us more about the role and control of pinnipeds than could the most extensive studies in unbounded seals or the most elaborate models in the largest computers (p. 75)." Similarly, Markussen & Øritsland (1991) proposed using captive seals in "penned in skerries and sounds", where diet could be tightly controlled, prey selection and handling could be directly observed, and "small-scale ecological community relations" could be experimentally examined.

Regardless of the scientific approach chosen to answer specific management questions, it is clear that there is a need for long-term studies of pinniped bioenergetics, which will likely yield results unattainable by short-term investigations. The present study illustrates that substantial changes occur throughout the year in many aspects of the harbour seals' energy budgets. The physiological adaptations that allow seals to prosper in their environment can only be properly understood when examined as a complex set of interactions within the context of their annual life cycle. Studies that document energetic parameters for short periods will oversimplify the seasonal changes occurring, resulting in misrepresentative or incomplete conclusions.

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Appendix A - Conversion coefficients

Conversion coefficients are given for various measures of energy and power. The conversions for O_2 consumption to energy are based upon an RQ of 0.80.

Energy	kJ	kcal	litre O_2
1 kJ	1.000	0.239	0.050
1 kcal	4.186	1.000	0.208
1 litre O_2	20.093	4.800	1.000

Power	Watt	kJ/d	mlO_2/min
1 Watt	1.000	86.400	2.987
1 kJ/d	0.012	1.000	0.035
1 mlO_2/min	0.335	28.930	1.000

Appendix B - Derivation of Truncated Cone Model

Given that the volume of a cone is:

$$\tfrac{1}{3}\pi r^2 L \qquad \text{[formula 1]}$$

Section *a* to *b* of a seal trunk is the difference between the cone of height=L, and the cone of height=L-h (where h equals the distance between points a and b; Figure B-1).

Volume of section = $\tfrac{1}{3}\pi r_a^2 L - \tfrac{1}{3}\pi r_b^2 (L-h)$ [formula 2]

Given the geometric relationship that:

$$\frac{r_a}{L} = \frac{r_b}{L-h} \qquad \text{[formula 3]}$$

Therefore:

$$L = \frac{hr_a}{r_a - r_b} \qquad \text{[formula 4]}$$

Substituting formula 4 into formula 2:

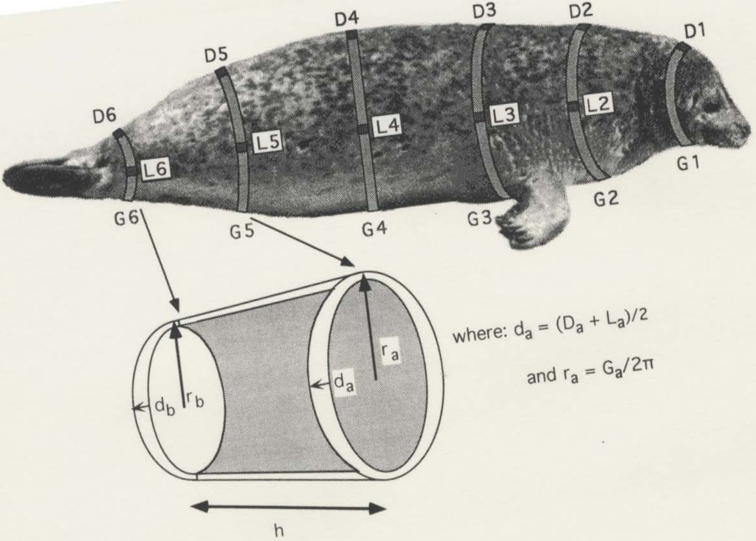
$$\tfrac{1}{3}\pi r_a^2 \frac{hr_a}{r_a - r_b} - \tfrac{1}{3}\pi r_b^2 \left(\frac{hr_a}{r_a - r_b} - h\right) \qquad \text{[formula 5]}$$

Which reduces to:

$$\tfrac{1}{3}\pi h (r_a^2 + r_a r_b^2 + r_b^2) \qquad \text{[formula 6]}$$

Figure B-1:

Derivation of blubber volume from truncated cone model. The model used is slightly different from the one proposed by Gales & Burton (1987), as dorsal and lateral blubber depths were used to estimate average blubber depth. The blubber volume was calculated from 5 sets of truncated cones, one representing total blubber volume, the other representing core volume. The blubber anterior to the pinnae and posterior to the rear ankle were disregarded, as were the foreflippers. Labesl are as designated: G = girth, D = dorsal blubber depth, and L = lateral blubber depth. The calculations in this Appendix were derived from the volume of a cone of height h, truncated to height h-L.



where: $d_a = (D_a + L_a)/2$

and $r_a = G_a/2\pi$

Given that the volume of the inner (core) section is almost identical to the volume of the total section, except that the radius equals r-d (where d is average fat depth), the volume of the inner section can be written as:

$$\tfrac{1}{3}\pi h[(r_a-d_a)^2+(r_a-d_a)(r_b-d_b)+(r_b-d_b)^2] \qquad \text{[formula 7]}$$

Subtracting inner cone [formula 6] from outer cone [formula 7] yields the volume of the blubber layer [formula 8]:

$$\tfrac{1}{3}\pi h[(r_a{}^2+r_ar_b{}^2+r_b{}^2)-((r_a-d_a)^2+(r_a-d_a)(r_b-d_b)+(r_b-d_b)^2)]$$

This equation reduces to:

$$\tfrac{1}{3}\pi h[2r_ad_a+2r_bd_b+r_ad_b+r_bd_a-d_a{}^2-d_b{}^2-d_ad_b] \qquad \text{[formula 9]}$$

However, radius (r) was derived from girth measurements (G) given the relationship that:

$$r_x=\frac{G_x}{2\pi} \qquad \text{[formula 10]}$$

Substituting formula 10 into formula 9 yields:

$$\tfrac{1}{3}\pi h[2(\tfrac{G_a}{2\pi})d_a+2(\tfrac{G_b}{2\pi})d_b+(\tfrac{G_a}{2\pi})d_b+(\tfrac{G_b}{2\pi})d_a-d_a{}^2-d_b{}^2-d_ad_b] \qquad \text{[formula 11]}$$

Which reduces to:

$$\tfrac{1}{3}\pi h[(\tfrac{G_a}{\pi})d_a+(\tfrac{G_b}{\pi})d_b+(\tfrac{G_a}{2\pi})d_b+(\tfrac{G_b}{2\pi})d_a-d_a{}^2-d_b{}^2-d_ad_b] \qquad \text{[formula 12]}$$

Appendix C - Calculating NE_P from Mass Changes

Energy Density of Tissues:

When determining the energetic contribution of changes in body mass to the overall energy budget, two factors must be taken into account: the relative contribution of each body component (i.e., blubber, core tissues, viscera) to total mass changes and the energetic density of those same components. The most reliable method to obtain the latter is through dissection and carcass composition analysis. Unfortunately, relevant data are sparse, and consistency among studies is poor.

Gales *et al.* (1994) examined body composition in 26 harp seals (Table C-1). Using an energy density for fat and protein of 39.33 and 17.99 kJ/g (wet weight), respectively (Schmidt-Nielsen 1990), the energy density of the blubber, viscera, and carcass is calculated to be 34.85, 4.91, and 5.64 kJ/g, respectively. In a similar fashion, values of 28.86, 5.08, and 7.37 kJ/g can be derived from data reported by Reilly & Fedak (1990) for the energy densities of the blubber, viscera, and carcass of 8 grey seals.

In comparison, Worthy (1987), in a simulation model of harp and gray seal energetics, used values of 39.48 kJ/g for the energy density of blubber, and 9.95 kJ/g and 5.72 kJ/g for carcass energy densities of harp and grey seals, respectively. However, these values were originally obtained from fasting pups (Worthy & Lavigne 1983a; 1983b; 1987). Slip *et al.* (1992) used energy densities of 35.4 and 10.9 kJ/g for the blubber and carcass of southern elephant seals (recalculated from their data). Sakamoto *et al.* (1989) used values of 37.46 and 9.84 kJ/g for the blubber and carcass of northern elephant seals, and Olesiuk (1993) used values of 37.8 and 6.5kJ/g for harbour seals. Brodie (1975) gave a figure of 37.8 kJ/g for the energy density of blubber in grey whales.

When no direct proximate composition analyses are available an appropriate tissue energy density value must be calculated from among previously published reports of tissue

Table C-1:

Body composition estimates for harp and grey seals. The data are broken down by average (±S.D.) percent wet weight for blubber, viscera, and carcass portions. Data in the upper portion are derived from Reilly & Fedak (1990) for 8 grey seals. Data in the lower portion are derived from Gales *et al.* (1994) for 26 harp seals.

Grey seals:

Component	Water	Ash	Fat	Protein
Blubber	21.0±9.4	0.38±0.18	68.9±13.4	9.8±4.1
Viscera	74.7±2.7	1.19±0.08	3.5±3.5	20.6±1.7
Carcass	64.8±3.5	4.13±0.50	8.4±5.4	22.6±2.4

Harp seals:

Component	Water	Ash	Fat	Protein
Blubber	9.5±3.1	0.01±0.04	87.7±4.1	2.0±1.0
Viscera	73.3±1.8	0.09±0.02	1.6±0.4	23.8±1.8
Carcass	68.3±1.8	4.4±1.3	3.6±1.2	23.5±1.0

composition. However, studies using the same composition data do not always report the same tissue energy density values. Boyd & Duck (1991) and Boyd *et al.* (1993), using data from Reilly & Fedak (1990), calculated values of 39.5 kJ/g and 23.5 kJ/g for body fat and body protein, respectively, for a study of Antarctic fur seals and southern elephant seals. Markussen *et al.* (1992b), working from the same data, calculated energy densities of 39.0 and 9.6 kJ/g for blubber and lean body mass, for a study with harbour seals. For the purposes of this study the values given for harp seals by Gales *et al.* (1994) were used for the tissue compositions of the harbour seals. This study reports exact tissue composition (rather than just energy density) and the energy densities they represent are intermediate to most published figures for phocid species.

Body Component Mass Changes:

The nature of the morphological data obtained in this study prohibited determining the degree to which the carcass and the viscera contributed to weight changes in the core tissues. It has been noted that, at least in cetaceans, certain internal organs (e.g. kidney) display mass changes induced by changes in nutritional state (Lockyer 1993). However, these changes are associated with changes in visceral fat deposits, and phocids generally have minimal dissectable lipid associated with internal organs (Beck *et al.* 1993b). Therefore, for the purposes of this study, all core mass changes were assumed to derive from the carcass.

The morphological data provided an estimate of the proportion of total mass change that derived from changes in the core (%core) or blubber (%blubber) components (Chapter 4; Table C-2). An appropriate estimate for the proximate composition of these tissues was also chosen. It is assumed that none of the observed changes in mass were due to compositional changes in the tissues, including their hydration state (Ortiz 1987; Beck *et al.* 1993b; although see Bowen *et al.* 1992). Therefore, the amount of energy needed to increase body mass by 1 g (NE_P^+) can be calculated by multiplying the proportion of fat

Table C-2:

Proportion of body mass changes due to changes in blubber mass. The slope (representing proportion of mass changes due to blubber changes) and the variance accounted for by the regression lines relating changes in total body mass to changes in calculated blubber mass (i.e., body mass = blubber mass x slope + b). Separate linear regressions are calculated for periods of body mass increase and decrease, 1992 and 1993 years combined. All regression lines were statistically significant at alpha ≤ 0.01.

Subject	Mass Increase	Mass Decrease
Male 1	slope = .891	slope = .806
	$r^2 = .83$	$r^2 = .88$
Male 2	slope = .882	slope = .776
	$r^2 = .63$	$r^2 = .62$
Male 3	slope = .765	slope = .785
	$r^2 = .68$	$r^2 = .53$
Male 4	slope = .865	slope = .640
	$r^2 = .54$	$r^2 = .39$
Male 5	slope = 0.458	slope = 1.500
	$r^2 = .68$	$r^2 = .29$
Female	slope = 0.823	slope = 1.078
	$r^2 = .84$	$r^2 = .80$

and protein in the blubber and core tissues ($\%F_B$, $\%P_B$, $\%F_C$, and $\%P_C$,) with the energetic cost producing 1 g of fat ($E_F{}^+$) or protein ($E_P{}^+$), factoring in the proportion of total mass changes that derive from those components (%blubber and %core). It can be represented by:

$$NE_P{}^+ = \%blubber*((\%F_B*E_F{}^+)+(\%P_B*E_P{}^+))+\%core*((\%F_C*E_F{}^+)+(\%P_C*E_P{}^+)).$$

[formula 1]

Similarly, the energy derived from the utilization of 1 g of body mass ($NE_P{}^-$) may be written as:

$$NE_P{}^- = \%blubber*((\%F_B*E_F{}^-)+(\%P_B*E_P{}^-))+\%core*((\%F_C*E_F{}^-)+(\%P_C*E_P{}^-))$$

[formula 2]

where $E_F{}^-$ and $E_P{}^-$ represent the energy derived from utilizing 1 g of fat or protein body mass, respectively.

Many studies of pinniped bioenergetics have ignored the cost of mass formation and the efficiency of body mass utilization. There is a tendency to multiply the reported energy density of these tissue by the wet weight of the estimated mass change. Assuming a perfect conversion from energy to mass and back again will provide either a maximum deduction from (in the case of mass gain) or contribution to (for mass loss) the animal's total energy budget.

However, there is a cost in the construction of body tissues and an inherent entropy in the conversion of these tissues back into metabolic energy ($E_X{}^+$ and $E_X{}^-$ respectively in the above equations). In addition, the efficiency with which food energy is converted to body mass is dependent upon both the composition of the nutrient source and the nutritional state and age of the animal.

Table C-3:

The theoretical efficiency (J/J) with which the energy of nutrients is employed in the synthesis of various body products. Efficiencies are calculated from the stoichiometry of transport and synthesis. From Blaxter (1989).

Dietary Substrate	Product	Estimated Efficiency	Heat Increment
Carbohydrate	Glycogen	0.95	0.05
	Body fat	0.80	0.20
Lipid	Body fat	0.96	0.04
Protein	Body fat	0.66	0.33
	Body protein	0.86	0.14

Blaxter (1989) summarized estimates of conversion efficiencies for various food substrates (Table C-3). These values were derived from "theoretical, biochemical efficiencies", that is, from a stoichiometric analysis of their biochemical composition. In most cases there is good agreement between these theoretical values and those obtained experimentally. For example, the experimentally observed efficiency for fat synthesis from ingested glycogen is 0.78, close to the theoretical value of 0.80. The experimentally observed efficiency with which fat is laid down by dietary lipids is approximately 0.85, versus the theoretical value of 0.95 (Wood 1984). However, the agreement between the theoretical (0.85) and experimental (as low as 0.44) efficiencies for converting dietary to body protein is poor. This difference has often been attributed to a high level of protein turnover in the body (although see Fuller *et al.* 1987).

In most experiments with simple-stomached species ingesting mixed composition diets, the observed efficiency of fat deposition from NE is consistently around 0.76. Values for the efficiency of protein deposition are much more variable, although a value of 0.56 is usually taken as representative (Agricultural Research Council 1981; Blaxter 1989).

Combining these efficiencies with the theoretical energy densities of lipid and protein (Schmidt-Nielsen 1990) it would take an estimated 51.750 kJ to deposit 1 g of lipid (39.33 kJ/0.76). Similarly, it would take 32.125 kJ to deposit 1 g of protein (17.99 kJ/0.56).

Incorporating the proximate composition values from Gales *et al.* (1994) with formula 1, the cost in NE of depositing 1 g of blubber is:

$$NE_P^{+}=1.00[(.877*51.750)+(.020*32.125)] = 46.03 \text{ kJ}$$

The cost of depositing 1 g of carcass is:

$$NE_P^{+}=1.00[(.036*51.750)+(.235*32.125)] = 9.41 \text{ kJ}$$

Both of the above examples utilize only half of the equation (the other half equals zero). Use of the full equation will calculate the NE needed to put on 1 g of body mass, given a known proportion of blubber and core tissue gain.

Conversion of body mass to available energy can be more complicated. Most studies, however, simplify the process and assume that all of the energy represented by body tissues can be utilized without additional cost (e.g., Worthy 1987). This oversimplification will overestimate the contribution of mass changes to available energy, as utilization of body components as an energy source will result in biochemical and thermal byproducts. However, as many of these costs are either extremely difficult to quantify or are already partially incorporated into other aspects of the energy budget (e.g., basal metabolism), this study follows this simplified scheme.

Therefore, by incorporating the proximate composition into formula 2, the energy derived from the utilization of 1 g of blubber would be:

$$NE_{p}^{-}=1.00[(.877*39.33)+(.020*17.99)] = 34.85\text{ kJ.}$$

Similarly, the energy derived from 1 g of core tissues would be:

$$NE_{p}^{-}=1.00[(.036*39.33)+(.235*17.99)] = 5.64\text{ kJ.}$$

A more complete example is provided by calculating the energy contributed to available energy when an animal loses 7.5 kg during a week. This example uses a hypothetical value of 83% for the proportion of mass loss derived from the blubber layer and 17% from the carcass (in practice, these values were determined through morphological modeling; see Chapter 4 and Table C-2). The total estimated energy released by this mass loss would be:

$$\begin{gathered}NE_{p}^{-} = 7500*(0.83[(.877*39.33)+(.020*17.99)] \\ +0.17[(.036*39.33)+(.235*17.99)]) = 224.15\text{ MJ.}\end{gathered}$$

Appendix D - Schedule of metabolic testing

Only those tests with useable results are given (i.e., trials with equipment failures and acclimation periods are ommitted). Dates and day of the year (DOY) are given for the start of the trial. Mass of the seals at the start of the trials (kg) is also given.

Date	DOY	Mass	Subject
14 Jul 1992	195	80.5	Male 2
21 Jul 1992	202	86.5	Male 1
23 Jul 1992	204	84.0	Male 3
04 Aug 1992	216	41.0	Male 5
11 Aug 1992	223	70.0	Male 2
18 Aug 1992	230	72.5	Male 4
21 Aug 1992	233	42.5	Male 5
25 Aug 1992	237	89.0	Male 1
01 Sep 1992	244	84.5	Male 3
03 Sep 1992	246	75.5	Female
06 Sep 1992	249	42.5	Male 5
08 Sep 1992	251	74.5	Male 2
17 Sep 1992	260	94.0	Male 1
22 Sep 1992	265	90.0	Male 3
27 Sep 1992	270	44.5	Male 5
29 Sep 1992	272	85.5	Female
01 Oct 1992	274	77.5	Male 2
15 Oct 1992	288	87.7	Male 3
20 Oct 1992	293	91.5	Female
27 Oct 1992	300	80.2	Male 4
28 Oct 1992	301	105.0	Male 1
29 Oct 1992	302	76.0	Male 2
03 Nov 1992	307	84.4	Male 3
06 Nov 1992	310	91.0	Female
12 Nov 1992	316	105.6	Male 1

19 Nov 1992	323	81.8	Male 2
24 Nov 1992	328	78.8	Male 4
26 Nov 1992	330	49.0	Male 5
01 Dec 1992	335	88.2	Male 3
03 Dec 1992	337	89.0	Female
09 Dec 1992	343	107.8	Male 1
15 Dec 1992	349	86.6	Male 2
22 Dec 1992	356	49.2	Male 5
30 Dec 1992	364	73.4	Male 4
05 Jan 1993	5	91.6	Male 3
12 Jan 1993	12	91.2	Female
19 Jan 1993	19	103.0	Male 1
21 Jan 1993	21	48.4	Male 5
26 Jan 1993	26	75.6	Male 4
28 Jan 1993	28	86.0	Male 2
02 Feb 1993	34	87.6	Female
08 Mar 1993	67	88.4	Female
09 Mar 1993	68	78.4	Male 4
18 Mar 1993	77	90.2	Male 3
29 Mar 1993	88	99.2	Male 1
30 Mar 1993	89	49.4	Male 5
31 Mar 1993	90	85.4	Male 2
07 Apr 1993	97	78.6	Female
13 Apr 1993	103	89.8	Male 3
15 Apr 1993	105	80.8	Male 4
20 Apr 1993	110	102.2	Male 1
22 Apr 1993	112	50.2	Male 5
27 Apr 1993	117	91.2	Male 2
30 Apr 1993	120	75.0	Female
01 May 1993	121	84.3	Male 3
04 May 1993	124	85.0	Male 4
11 May 1993	131	103.8	Male 1
20 May 1993	140	98.2	Male 2
21 May 1993	141	50.8	Male 5
25 May 1993	145	74.6	Female

28 May 1993	148	101.2	Male 3
06 Jun 1993	157	88.2	Male 4
07 Jun 1993	158	101.4	Male 1
08 Jun 1993	159	98.6	Male 2
09 Jun 1993	160	52.8	Male 5
06 Jul 1993	187	77.4	Female
09 Jul 1993	190	53.7	Male 5
13 Jul 1993	194	84.2	Male 3
22 Jul 1993	203	79.2	Male 2
26 Jul 1993	207	75.6	Male 4
27 Jul 1993	208	80.6	Male 1
02 Aug 1993	214	57.2	Male 5
09 Aug 1993	221	71.0	Female
10 Aug 1993	222	72.8	Male 3
16 Aug 1993	228	79.2	Male 2
23 Aug 1993	235	81.0	Male 1
24 Aug 1993	236	75.2	Male 4
30 Aug 1993	242	52.6	Male 5
07 Sep 1993	252	76.4	Male 3
08 Sep 1993	253	67.8	Female
15 Sep 1993	260	76.4	Male 2
21 Sep 1993	266	82.0	Male 1
22 Sep 1993	267	75.8	Male 4
04 Oct 1993	277	52.0	Male 5
06 Oct 1993	279	78.4	Male 3
12 Oct 1993	285	76.6	Female
13 Oct 1993	286	79.0	Male 2
26 Oct 1993	299	81.2	Male 4
02 Nov 1993	306	85.0	Male 3

Appendix E - Results of metabolic determinations

The date and day of the year (DOY) are given for the start of the trial. Metabolism is presented in several formats, including as a multiple of the value predicted by Kleiber (1975) for basal metabolism for adult terrestrial mammals.

Male 1:

Date	DOY	Mass	mlO_2/min	$kJ \times kg^{-1} \times d^{-1}$	$mlO_2 \times min^{-1} \times kg^{-1}$	kJ/d	Multiple of Kleiber
21 Jul 1992	203	86.5	433.7	145.1	5.01	12550	1.51
25 Aug 1992	238	89.0	493.0	160.3	5.54	14264	1.68
17 Sep 1992	261	94.0	418.9	128.9	4.46	12119	1.37
28 Oct 1992	302	105.0	232.9	64.2	2.22	6738	0.70
12 Nov 1992	317	105.6	250.2	68.6	2.37	7239	0.75
9 Dec 1992	344	107.8	286.3	76.8	2.66	8284	0.85
19 Jan 1993	19	103.0	438.8	123.2	4.26	12695	1.34
29 Mar 1993	88	99.2	401.1	117.0	4.04	11605	1.26
20 Apr 1993	110	102.2	371.1	105.1	3.63	10737	1.14
11 May 1993	131	103.8	311.2	86.8	3.00	9005	0.95
7 Jun 1993	158	101.4	261.2	74.5	2.58	7556	0.81
27 Jul 1993	208	80.6	305.1	109.5	3.79	8828	1.12
23 Aug 1993	235	81.0	243.9	87.1	3.01	7057	0.89
21 Sep 1993	266	82.0	224.6	79.3	2.74	6500	0.81

Male 2:

Date	DOY	Mass	mlO$_2$/min	kJ x kg^{-1} x d^{-1}	mlO$_2$ x min^{-1} x kg^{-1}	kJ/d	Multiple of Kleiber
14 Jul 1992	196	80.5	389.2	139.9	4.83	11261	1.43
11 Aug 1992	224	70.0	389.7	161.1	5.57	11275	1.59
8 Sep 1992	252	74.5	436.6	169.6	5.86	12632	1.70
1 Oct 1992	275	77.5	373.0	139.3	4.81	10792	1.41
29 Oct 1992	303	76.0	367.6	139.9	4.84	10635	1.41
19 Nov 1992	324	81.8	333.3	117.9	4.07	9644	1.21
15 Dec 1992	350	86.6	370.9	123.9	4.28	10731	1.29
28 Jan 1993	28	86.0	434.7	146.3	5.05	12578	1.52
31 Mar 1993	90	85.4	503.6	170.6	5.90	14570	1.77
27 Apr 1993	117	91.2	496.1	157.4	5.44	14355	1.66
20 May 1993	140	98.2	401.2	118.2	4.09	11609	1.27
8 Jun 1993	159	98.6	440.5	129.2	4.47	12744	1.39
22 Jul 1993	203	79.2	403.3	147.3	5.09	11669	1.50
16 Aug 1993	228	79.2	438.3	160.1	5.53	12680	1.63
15 Sep 1993	260	76.4	405.6	153.6	5.31	11737	1.55
13 Oct 1993	286	79.0	362.3	132.7	4.59	10482	1.35

Female:

Date	DOY	Mass	mlO_2/min	kJ x kg^{-1} x d^{-1}	mlO_2 x min^{-1} x kg^{-1}	kJ/d	Multiple of Kleiber
3 Sep 1992	247	75.5	282.7	108.3	3.74	8181	1.09
29 Sep 1992	273	85.5	224.4	75.9	2.62	6492	0.79
20 Oct 1992	294	91.5	222.6	70.4	2.43	6441	0.74
6 Nov 1992	311	91.0	226.2	71.9	2.49	6544	0.76
3 Dec 1992	338	89.0	277.9	90.3	3.12	8041	0.95
12 Jan 1993	12	91.2	373.6	118.5	4.10	10809	1.25
2 Feb 1993	34	87.6	353.8	116.8	4.04	10236	1.22
8 Mar 1993	67	88.4	362.0	118.5	4.10	10475	1.24
7 Apr 1993	97	78.6	403.7	148.6	5.14	11680	1.51
30 Apr 1993	120	75.0	356.2	137.4	4.75	10306	1.38
25 May 1993	145	74.6	303.3	117.7	4.07	8777	1.18
6 Jul 1993	187	77.4	340.9	127.4	4.40	9864	1.29
9 Aug 1993	221	71.0	344.3	140.3	4.85	9962	1.39
8 Sep 1993	253	67.8	306.3	130.7	4.52	8862	1.28
12 Oct 1993	285	76.6	306.8	115.9	4.01	8877	1.17

Male 3:

Date	DOY	Mass	mlO_2/min	kJ x kg^{-1} x d^{-1}	mlO_2 x min^{-1} x kg^{-1}	kJ/d	Multiple of Kleiber
23 Jun 1992	175	92.0	409.1	128.7	4.45	11838	1.36
23 Jul 1992	205	84.0	446.8	153.9	5.32	12927	1.59
1 Sep 1992	245	84.5	434.7	148.8	5.14	12577	1.54
22 Sep 1992	266	90.0	411.3	132.2	4.57	11901	1.39
15 Oct 1992	289	87.7	377.3	124.5	4.30	10917	1.30
3 Nov 1992	308	84.4	369.4	126.6	4.38	10689	1.31
1 Dec 1992	336	88.2	361.4	118.6	4.10	10457	1.24
5 Jan 1993	5	91.6	380.8	120.3	4.16	11019	1.27
13 Feb 1993	44	91.0	501.3	159.4	5.51	14504	1.68
18 Mar 1993	77	90.2	637.3	204.4	7.07	18439	2.15
13 Apr 1993	103	89.8	481.5	155.2	5.36	13933	1.63
1 May 1993	121	84.3	450.8	154.7	5.35	13043	1.60
28 May 1993	148	101.2	468.5	134.0	4.63	13557	1.45
13 Jul 1993	194	84.2	371.6	127.7	4.41	10751	1.32
10 Aug 1993	222	72.8	330.6	131.4	4.54	9567	1.31
7 Sep 1993	252	76.4	311.4	117.9	4.08	9011	1.19
6 Oct 1993	279	78.4	317.5	117.2	4.05	9187	1.19
2 Nov 1993	306	85.0	442.3	150.6	5.20	12796	1.56

Male 4:

Date	DOY	Mass	mlO_2/min	$kJ \times kg^{-1} \times d^{-1}$	$mlO_2 \times min^{-1} \times kg^{-1}$	kJ/d	Multiple of Kleiber
18 Aug 1992	231	72.5	472.4	188.6	6.52	13669	1.88
15 Sep 1992	259	79.5	402.7	146.6	5.07	11651	1.49
27 Oct 1992	301	80.2	345.6	124.7	4.31	9998	1.27
24 Nov 1992	329	78.8	404.1	148.4	5.13	11691	1.51
30 Dec 1992	365	73.4	586.4	231.2	7.99	16967	2.31
26 Jan 1993	26	75.6	529.2	202.5	7.00	15311	2.04
15 Apr 1993	105	80.8	466.6	167.1	5.77	13501	1.71
4 May 1993	124	85.0	391.5	133.3	4.61	11328	1.38
6 Jun 1993	157	88.2	397.5	130.4	4.51	11500	1.36
26 Jul 1993	207	75.6	372.8	142.7	4.93	10785	1.44
24 Aug 1993	236	75.2	470.1	180.9	6.25	13601	1.82
22 Sep 1993	267	75.8	334.9	127.8	4.42	9690	1.29
26 Oct 1993	299	81.2	387.2	138.0	4.77	11202	1.41

Male 5:

Date	DOY	Mass	mlO_2/min	$kJ \times kg^{-1} \times d^{-1}$	$mlO_2 \times min^{-1} \times kg^{-1}$	kJ/d	Multiple of Kleiber
4 Aug 1992	217	41.0	370.8	261.7	9.04	10730	2.26
21 Aug 1992	234	42.5	357.4	243.3	8.41	10340	2.12
6 Sep 1992	250	42.5	328.7	223.8	7.73	9511	1.95
27 Sep 1992	271	44.5	249.5	162.2	5.61	7219	1.43
26 Nov 1992	331	49.0	365.7	216.0	7.46	10582	1.95
22 Dec 1992	357	49.2	389.4	229.0	7.92	11268	2.07
21 Jan 1993	21	48.4	546.4	326.6	11.3	15808	2.94
30 Mar 1993	89	49.4	434.0	254.2	8.79	12558	2.30
22 Apr 1993	112	50.2	399.2	230.1	7.95	11550	2.09
21 May 1993	141	50.8	397.0	226.1	7.81	11486	2.06
9 Jun 1993	160	52.8	355.1	194.6	6.72	10274	1.79
9 Jul 1993	190	53.7	425.9	229.5	7.93	12323	2.12
2 Aug 1993	214	57.2	412.[illegible]	208.8	7.22	11945	1.96
30 Aug 1993	242	52.6	478.7	263.3	9.10	13850	2.42
4 Oct 1993	277	52.0	353.0	196.4	6.79	10213	1.80