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Seasonal energetics of northern phocid seals

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ABSTRACT

The metabolic rate of harp (*Pagophilus groenlandicus*), harbor (*Phoca vitulina*), and ringed seals (*Pusa hispida*) was measured at various temperatures in air and water to estimate basal metabolic rates (BMRs) in these species. The basal rate and body composition of three harp seals were also measured throughout the year to examine the extent to which they vary seasonally. Marine mammalian carnivores generally have BMRs that are over three times the rates expected from body mass in mammals generally, both as a response to a cold-water distribution and to carnivorous food habits with the basal rates of terrestrial carnivores averaging about 1.8 times the mean of mammals. Phocid seals, however, have basal rates of metabolism that are 30% lower than other marine carnivores. Captive seals undergo profound changes in body mass and food consumption throughout the year, and after accounting for changes in body mass, the lowest rate of food intake occurs in summer. Contrary to earlier observations, harp seals also have lower basal rates during summer than during winter, but the variation in BMR, relative to mass expectations, was not associated with changes in the size of fat deposits. The summer reduction in energy expenditure and food consumption correlated with a reduction in BMR. That is, changes in BMR account for a significant portion of the seasonal variation in energy expenditure in the harp seal. Changes in body mass of harp seals throughout the year were due not only to changes in the size of body fat deposits, but also to changes in lean body mass. These results suggest that bioenergetics models used to predict prey consumption by seals should include time-variant energy requirements.

1. Introduction

Our collective understanding of the level of energy expenditure of marine mammals has changed over the years. A major point of controversy has been whether an aquatic existence, especially in cold water, results in elevated rates of energy expenditure during resting (Irving, 1969). Although the first measurements suggested phocid seals (Family Phocidae) had higher rates of metabolism than terrestrial mammals of the same mass (Irving et al., 1935; Scholander, 1940; Scholander et al., 1942; Irving and Hart, 1957; Hart and Irving, 1959; Kooyman et al., 1973; Miller and Irving, 1975; Miller et al., 1976), some researchers later postulated that the high rates were a result of using forcibly restrained and/or immature animals (Lavigne et al., 1982; Schmitz and Lavigne, 1984; Lavigne et al., 1986; Boyd, 2002). More recent studies, however, have reported high rates of metabolism for pinnipeds even when measurements were taken while conforming to basal conditions (Boily and Lavigne, 1997; Costa and Williams, 1999; Costa, 2001; Williams et al., 2001; Boyd, 2002; Williams and Worthy, 2002). Furthermore, measurements on sea otters (*Enhydra lutris*) demonstrated relatively high rates of metabolism (Morrison et al., 1974; Costa and Kooyman, 1982), as did measurements on California sea lions (*Zalophus californianus*) (Hurley and Costa, 2001) and cetaceans (Kanwisher and Sundnes, 1965; Williams et al., 2001).

Basal rate of metabolism (BMR) in mammals correlates chiefly with body mass, although other factors such as climate, an aquatic or terrestrial existence, and food habits also influence BMR (McNab, 2002, 2008). The relationship between body mass and BMR was mainly derived from comparing species, occasionally individuals of the same species, but usually not within individuals. Pinnipeds, however, often show marked seasonal variations in body mass, which raises the question whether changes in BMR reflect changes in the size of adipose tissue (Rea and Costa, 1992; Costa and Williams, 1999), which is usually thought to have a relatively low energy demand.

Northern phocid seals live in a highly seasonal environment and, consequently, some aspects of their life history demonstrate a high level of circannual periodicity. For example, harp seals in the northwest Atlantic migrate south preceding the advance of pack ice in fall and return north following the ice retreat in spring. These seals spend winter in the southern portion of their range, where they congregate in huge herds to give birth on pack ice from late February to early March (Ronald and Healey, 1981; Bowen and Sergeant, 1983).

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Most phocids do not forage during the breeding season, summer (Sergeant, 1991), although harbor seals do. Consequently, many phocids drastically decrease body mass during summer, even when fed *ad libitum* in captivity.

Given the profound variation in food intake and energy expenditure observed in pinnipeds in general, and phocids in particular, BMR may vary throughout the annual cycle, especially reflecting periods when food is scarce, of poor quality, or when other activities divert attention from feeding (Mrosovsky and Sherry, 1980). Therefore, BMR of harp seals might be expected to be maximal in winter when they encounter low temperatures and are rapidly gaining mass (Schusterman and Gentry, 1971; Rosen and Renouf, 1995, 1997, 1998), and lowest in summer when food consumption is lowest. Previous studies conducted at the Ocean Sciences Centre, however, concluded that harp seals had a higher BMR during spring and summer than in the rest of the year (Renouf and Gales, 1994; Hedd et al., 1997).

The objectives of this study were two-fold: 1) to determine BMR in harp, harbor, and ringed seals, and 2) to determine the seasonal variations of BMR in harp seals and its potential relationship with changes in body composition, food consumption, and energy expenditure. This was accomplished by measuring resting rates of metabolism over a range in ambient temperatures to define the zone of thermoneutrality when heat production is not increased to facilitate temperature regulation. Basal rates of metabolism are standardized measures in endotherms used for intra- and inter-specific comparisons. They are the rates of post-absorptive mature animals at rest under thermoneutral conditions during the inactive period, while not in a reproductive condition (McNab, 1997).

2. Materials and methods

2.1. Animals

Scientific names for harp seal (*Pagophilus groenlandicus*), harbor seal (*Phoca vitulina*), and ringed seal (*Pusa hispida*) follow Perry and Carr (1997), who pointed out that the genus *Phoca* (s.l.) is paraphyletic. Other scientific names follow Wilson and Reeder (1993). Rates of metabolism were measured in nine harp seals, three harbor seals, and one ringed seal. The two females were not in a reproductive condition. This study was conducted at the seal facility of the Ocean Sciences Centre (OSC), Memorial University of Newfoundland, in Logy Bay, Newfoundland (47°38′N, 52°40′W). The study protocols and facilities had been approved for conducting studies on seals by the appropriate animal care and use committee. Animals were kept outdoors in a facility consisting of two 12-m-diameter tanks (300-m^3 capacity each) and 190 m^2 of haul-out decking surrounding the tanks. The tanks were cleaned weekly and refilled with seawater pumped from the bay. Seals involved in this study had been kept captive for varying periods of time, all but one for at least a year at the commencement of the study. Seasonal variations in BMR were studied on three adult male harp seals. Animals were kept in 12-m diameter tanks of 3 m in water depth, which allowed the animals unrestrained activity.

2.2. Methods

Rates of metabolism were measured in terms of oxygen consumption through open-flow respirometry. Oxygen consumption was measured in post-absorptive (>16 h post-prandial) animals for periods of 2 to 4 h. All measurements were made during daylight hours, a potential non-conformance to standard conditions, but a circadian rhythm in resting rate may not be present (Boily and Lavigne, 1995), circadian rhythms being most highly developed in small species (McNab, 2009). Animals were monitored using a closed-circuit TV system to ensure they were inactive but awake during measurements.

To measure oxygen consumption in air, seals were placed in a chamber that had ambient temperature controlled. Animals were acclimatized to the chamber for periods of 2 to 4 h over two weeks before commencing measurements. The chamber was 2.4×1.0×0.9 m internally, with an empty volume of 2.16 m^3. It had two doors and a 11,000 BTU capacity temperature-control system. Oxygen consumption was measured at ambient temperatures from −12 to 25 °C to ensure that measurements occurred within the range of thermoneutrality, a basic requirement for obtaining valid estimates of BMR. Stomach temperature in harbor and harp seals was monitored while the animal was in the chamber with a temperature telemetry pill (38 g, 5.5×2.8-cm^2 diameter), given to a seal inside a herring during feeding the previous day. In many instances, pills stayed in the animal for several days. Pills were calibrated before administration and immediately after recovery.

Oxygen consumption of seals was also measured when they were in water. For this, a tank 1.8-m in diameter was filled with enough water to keep the seal submerged, but not enough to permit swimming. This tank was airtight and had been used for measurements of oxygen consumption by other researchers (Renouf and Gales, 1994; Hedd et al., 1997). The tank was filled with non-circulating seawater at temperatures between 0 and 3 °C pumped from nearby Logy Bay, NF, which was the range of temperatures at which "in-water" measurements were made.

Fresh air was pumped into both chambers at a rate of 100 to 150 L/min, depending on the size of the animal. Flow rate was measured using a Cole-Parmer gravimetric flowmeter (Vernon Hills, IL, USA). Given the large volume of air introduced into the chamber, no attempt was made to remove water before measuring airflow. Instead, the humidity of the incoming air was monitored continuously using a Cole-Parmer thermohygrometer, and the calculated volume of water vapor was subtracted from the volume of air introduced to the chamber. Copper-constantan thermocouples measured the temperature of air in the chambers and at the flowmeter.

A subsample of air was continuously drawn from the chamber at a rate of 150 mL/min. This sample first passed through soda lime and then silica gel to remove carbon dioxide and water, respectively. The content of oxygen in the sample was determined using a S-3A Applied Electrochemistry oxygen analyzer (Pittsburgh, PA, USA). The rate of oxygen consumption corresponded to a chamber oxygen concentration that was maintained constant for at least 10 min during the two- to four-hour measurement period using equation 10 of Depocas and Hart (1957).

Basal rates of metabolism were measured (10 to 18 per month) in three adult male harp seals (ELM, TYL, and VIR) in Fall (October), Winter (January), Spring (April), and Summer (July). This design permitted a comparison of BMR among seasons with enough replicate measurements per seal to provide robust conclusions. Differences in BMR among seasons were tested using generalized linear models that included "seal" as a factor and body mass as a covariate. BMR in other individuals and species was measured predominantly in winter.

The body composition of the same three adult harp seals (ELM, TYL, and VIR) was also estimated during each season. We estimated the water content of the body through isotope dilution (reviewed by Speakman, 1997). In early November, February, May, and July, each animal was physically restrained, after intramuscular administration of Valium (5 mg/mL, Roche Laboratories) at an approximate dose of 1.5 mL/100 kg, to facilitate handling. A known amount of deuterium oxide (D_2O, 99.9% purity, Cambridge Isotope Laboratories, Andover, MA, USA) was administered by gastric gavage, at an approximate dose of 0.5 g/kg. The complete delivery of the isotope was secured by flushing the syringe and stomach tube with small amounts of water and air.

Blood samples were drawn from the venous plexus of the hind flippers at approximately 5, 20, and 28 h after administration of the isotope. During this time, animals were fasted and kept on deck. Blood

Table 1
Total ($\dot{V}_{O_2}$) and mass-specific ($\dot{V}_{O_2}$/m) resting metabolic rates of individual harp (*Pagophilus groenlandicus*), harbor (*Phoca vitulina*), and ringed (*Pusa hispida*) seals

Seal	Sex	*N*	Age (months)	Body mass (kg)	$\dot{V}_{O_2}$ (L/h)	$\dot{V}_{O_2}$/m (mL/g h)	BMR (%)*
Harp seals							
BAB	f	11	>144	219.6±16.52	39.6±2.73	0.188±0.017	166
BRU	m	5	1	36.6±1.80	10.1±0.26	0.278±0.009	149
ELM	m	26	>144	134.5±3.11	31.2±1.20	0.232±0.008	179
JAM	m	4	37	71.0±0.84	20.1±3.52	0.285±0.053	184
MIC	m	4	>84	103.2±0.86	31.5±0.78	0.305±0.006	218
RHO	f	1	>84	117.0±0.00	35.9±0.00	0.307±0.000	228
TYL	m	36	81	168.3±3.78	25.4±1.03	0.152±0.006	124
VIC	m	5	45	173.2±12.20	39.6±2.68	0.229±0.008	190
VIR	m	29	>144	130.7±3.06	25.1±1.01	0.196±0.007	147
Harbor seals							
CAE	m	5	129	82.3±0.68	33.7±2.02	0.409±0.026	275
CLA	m	8	225	85.9±1.50	25.0±1.89	0.294±0.025	200
JUL	m	6	141	91.7±1.49	30.8±2.47	0.337±0.028	234
Ringed seal							
LER	m	7	81	46.6±3.44	13.8±0.56	0.303±0.019	174

*%=[100×V_{O_2}(mLO2/g h)]/3.50 g$^{-0.279}$ (McNab, 2008).

samples were allowed to clot, and the serum was then obtained and kept frozen at −70 °C until analysis. Water was obtained from plasma samples by distillation, using the method proposed by Oftedal and Iverson (1987). The concentration of deuterium oxide in the water samples was then determined through mass ratio spectrophotometry (Speakman, 1997).

Concentrations of D_2O in plasma were used to determine water pool size (P_o) of seals. Log-transformed serum concentrations of D_2O were regressed against time after administration of the isotope to calculate D_2O concentration at time of administration, C_o. This approach prevents the overestimation of water pool size that occurs when using the actual concentration of D_2O obtained after an equilibration time of 3 to 4 h (Oftedal and Iverson, 1987; Speakman, 1997). Then, water pool size was calculated from:

$$P_o = C_o \times D_2O \text{ administered.}$$

The method of isotope dilution produces accurate estimations of body composition: comparisons of total body water content with results from proximate composition analyses of carcasses of seals, have shown that the differences between the two approaches are less than 2% (Lydersen et al., 1992; Reilly and Fedak, 1990; Oftedal et al., 1993; Reilly et al., 1996; Webb et al., 1998; Bowen and Iverson, 1998).

Water pool size (P_o) was used to estimate lean body mass (LBM) using a ratio of 0.703 (P_o:LBM) determined by carcass analysis of adult harp seals (Gales et al., 1994). Body fat was determined as the difference between body mass and lean body mass. Gales et al. (1994) also found that 25.7% of LBM of adult harp seals was protein. The energy content of the body was estimated using the energy equivalencies of 38.91 kJ/g for fat and of 23.64 kJ/g for protein (Oftedal et al., 1987).

Seals were fed daily around 1200 h. Food consisted of thawed frozen herring supplemented with vitamins. Each animal was allowed to eat as much as it wanted for a period of 2 h. It was apparent this limited feeding period did not prevent adequate food intake because most seals maintained body mass within ranges observed in the wild. Furthermore, one female (BAB) that had whelped several times in captivity was considerably overweight. Seals were weighed using a suspended cage and an electronic scale accurate to 0.1 kg at approximately weekly intervals, thus allowing us to examine body mass changes with respect to changes in energy intake. We calculated daily mass change (DMC, g/d) as the difference between two consecutive weighings, divided by the days elapsed between them. Each batch of herring bought to feed the seals was analyzed for proximal composition. Accurate recording of the food consumed by each seal and chemical composition data of fish permitted estimating digestible energy intake of each individual animal. Digestible energy intake (DEI, MJ/d) was estimated from the average daily food intake measured between consecutive weighings multiplied by the energy content of herring and by its digestive efficiency (Lawson et al., 1997). Energy intake at constant body mass (i.e., maintenance energy intake, MEI, MJ/d) was calculated through regression analysis (*x* intercept of DMC regressed against DEI) for each of the different periods (i.e., seasons) in which each year was divided (Table 1).

Resting rates of metabolism in water and air were compared, as were measurements before and during moult, using paired *t*-tests of data collected from the same animals during the same season. The effect of body mass and age on resting rates was examined to compare them with those of terrestrial carnivorous mammals (McNab, 2000; Williams et al., 2001) and with a general standard developed from 639 species of wild mammals (McNab, 2008). Marine mammals have often been compared to the Kleiber (1961) curve, which is an inappropriately high standard developed from 12 domesticated species.

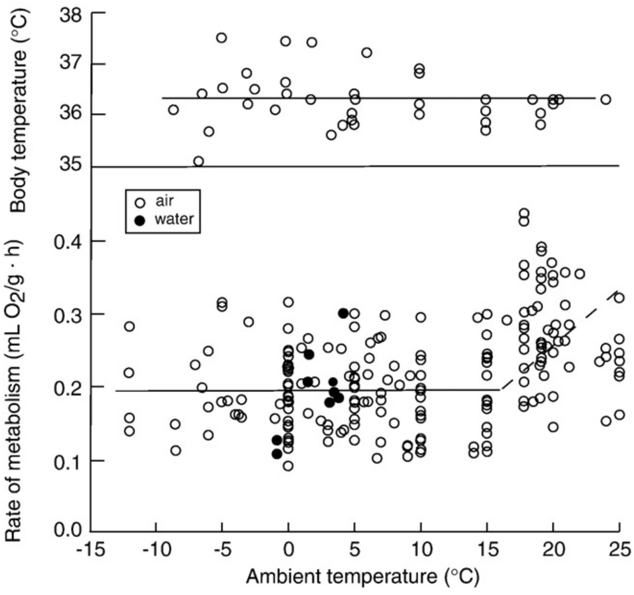

Fig. 1. Mass-specific rate of metabolism and body temperature in seven adult harp seals (*P. groenlandicus*) as a function of ambient temperature. Measurements were made both in air and water and at various times of the year.

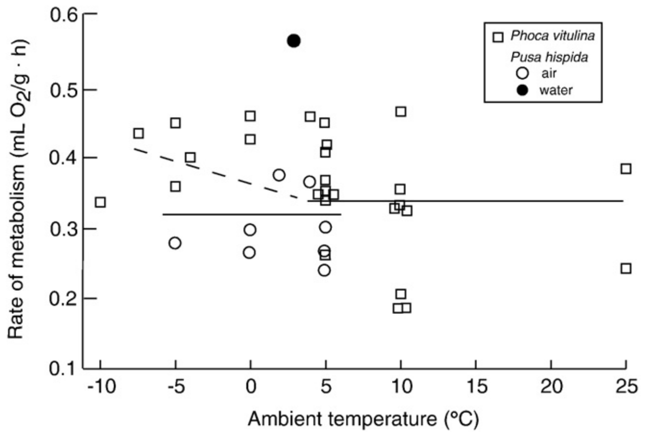

Fig. 2. Mass-specific rate of metabolism in three harbor seals (*P. vitulina*) and one ringed seal (*P. hispida*) as a function of ambient temperature. One measurement in water was made with the ringed seal, all other measurements were made in air. Measurements were made at various times of the year.

Table 2
Seasonal variations in BMR in three adult harp seals

Seal		Fall	Winter	Spring	Summer
ELM	Mass (kg)	119.2±0.23	141.9±0.47	166.5±0.81	136.4±0.85
	BMR (mL O_2/g h)	0.266±0.0072	0.229±0.002	0.228±0.0057	0.166±0.0055
	% All-mammal	198	179	186	128
TYL	Mass (kg)	141.4±0.22	167±0.62	176.2±0.67	136.8±0.26
	BMR (mL O_2/g h)	0.181±0.0048	0.128±0.0036	0.158±0.0069	0.134±0.0028
	% All-mammal	141	105	136	104
VIR	Mass (kg)	116±0.19	141.7±0.40	142.6±0.75	118±0.35
	BMR (mL O_2/g h)	0.213±0.0044	0.172±0.0028	0.214±0.0059	0.161±0.0044
	% All-mammal	158	134	168	120

The relationship among basal rate, body mass, and environment in mammalian carnivores was examined with ANCOVA. Body composition and BMR data were analyzed using a generalized linear model because measurements were concentrated over four evenly spaced, discrete periods during a year, thus obviating the need for more complex time series approaches.

3. Results

3.1. Basal rates of metabolism of northern phocids

Total rates of oxygen consumption of resting adult seals varied from 13.8 to 39.6 LO_2/h and mass-specific rates ranged from 0.15 to 0.41 mLO_2/g h (Table 1). Rates of oxygen consumption of harp seals in water and in air did not differ (paired *t*-test=−0.25, *df*=8, *P*=0.81) at temperatures between 0 and 3 °C (Fig. 1). However, the ringed seal increased its rate of metabolism by 54% while in water (Fig. 2) either because its small size allowed it to swim despite the small amount of water in the tank, or because the lower limit of thermoneutrality is higher when this small seal is immersed in water. The harbor seals were not measured in water. Rates of oxygen consumption of harp seals before and during moult did not differ (paired *t*-test=1.4, *df*=7, *P*=0.22).

Rates of metabolism in adult harp seals did not change with air temperature between −12 and 15 °C, but increased at T_as>15 °C (Fig. 1). Consequently, only values from T_as≤15 °C were used to estimate basal rate of metabolism in this species. In the harbor seal, rate of metabolism was not correlated with T_a ($F_{1,25}$=1.03, *P*=0.32), but a close examination suggests that a conservative estimate of basal rate is found between 5 and 25 °C, which is what is used here. The few data on the ringed seal are independent of T_as between −5 and 5 °C (Fig. 2).

The rate of metabolism in post-absorptive harp seals within the zone of thermoneutrality, subject to the potential influence of photoperiod, equals the basal metabolic rate of adult individuals (McNab, 1997). This rate can be estimated in two ways. If the data are pooled (Fig. 1), then the harp seal's mean basal rate equals 0.195±0.0053 mLO_2/g h (*n*=112), which given a mean pooled mass of 153.2 kg, is 155% of the value expected from the all-mammal curve. However, the best estimate from a population viewpoint would be the mean of individual means (McNab, 2003), which avoids the impact of an unequal number of measurements in the individuals. Then, the mean BMR of the seven adult harp seals equaled 0.229±0.021 mLO_2/g h, which at a mean mass of 149.5 kg is

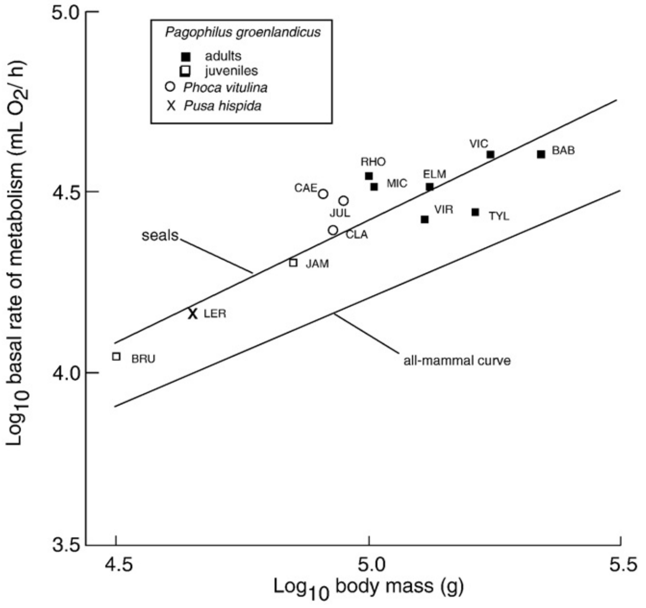

Fig. 3. Log_{10} BMR in the thirteen seals studied as a function of the log_{10} body mass. The fitted curve for these seals and the all-mammal curve (McNab, 2008) are both indicated. The individuals are identified by letters (see Table 1).

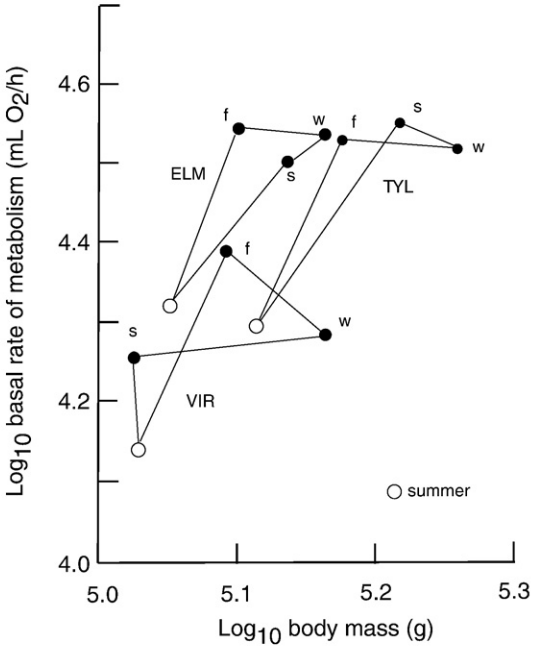

Fig. 4. Log_{10} BMR in three harp seals (VIR, ELM, TYL) during the year as a function of log_{10} body mass. The seasons are spring (s), summer (O), fall (f), and winter (w).

Table 3
Body composition of three adult harp seals throughout the year cycle

Seal	Season	Body mass (kg)	Lean body mass[a] %	Water[b] %	Fat[c] %	Protein[d] %	Other[e] %	Energy density[f] (MJ/kg)
ELM	Late fall	127.4	72.1	50.7	27.9	18.5	2.9	15.3
	Late winter	150.2	64.8	45.6	35.2	16.6	2.6	17.6
	Late spring	139.0	72.1	50.7	27.9	18.5	2.9	15.2
	Late summer	112.6	69.6	48.9	30.4	17.9	2.8	16.1
TYL	Late fall	153.2	53.3	37.5	46.7	13.7	2.1	21.4
	Late winter	188.8	54.0	38.0	46.0	13.9	2.1	21.2
	Late spring	169.6	61.1	43.0	38.9	15.7	2.4	18.8
	Late summer	133.1	53.3	37.5	46.7	13.7	2.1	21.4
VIR	Late fall	124.4	58.3	41.0	41.7	15.0	2.3	19.8
	Late winter	149.0	78.4	55.1	21.6	20.1	3.2	13.2
	Late spring	106.4	85.9	60.4	14.1	22.1	3.4	10.7
	Late summer	107.5	65.3	45.9	34.7	16.8	2.6	17.5

The amount of each of the different components is given in absolute (kg, MJ/kg) or relative term (percentage).

[a] LBM (%)=water (%)/0.703.

[b] Water (%)=$C_o \times D_2O$.

[c] Fat (%)=BM−LBM.

[d] Protein (%)=LBM×0.257.

[e] Other (%)=LMB−(water+fat+protein).

[f] Energy density=38.91 (kJ/g fat) (% fat/100) (1000 g/kg)+23.64 (kJ/g protein) (% protein/100) (1000 g/kg).

equivalent to a basal metabolic rate that is 182% of the value expected from the all-mammal curve.

In this study two individuals, BRU and JAM, which weighed 36.6 and 71.0 kg, respectively, were juveniles (Table 1). Juveniles in theory should not have basal rates because of the presumptive added cost of growth. However, these individuals had mean thermoneutral rates, corrected for body mass, that fell within the range of values found in adults (Table 1).

The mean BMR of three individual adult harbor seals (Fig. 2), derived as the mean of individual means, was 0.347±0.034 mLO$_2$/g h (N=3), which is 237% of the value expected from the all-mammal value for a mass of 86.8 kg, and indistinguishable from 0.338±0.099 mLO$_2$/g h (n=19), which is the mean pooled BMR. That is, no difference was found in BMR among the three individuals ($F_{3,9}$=0.92, P=0.47). The single ringed seal (Fig. 2), an adult, had a BMR equal to 0.303±0.028 mLO$_2$/g h (n=7), which is 174% of the value expected for its mass of 46.6 kg.

The basal rates obtained from the 13 individuals in this study conform to a mean seal curve (Fig. 3):

$$\dot{V}_{O_2}(\text{mLO}_2/\text{h}) = 11.61m^{0.670}, \qquad (1)$$

where m is mass in g. The two juvenile harp seals had thermoneutral rates that fell below the mean seal curve. That is, the thermoneutral rates in these juveniles were equivalent to the BMRs of the adults, which suggests that the juveniles showed no evidence of energy expenditure for growth.

Body temperature equaled 36.3±0.10 °C (n=40) in the harp seal, which was independent of T_a (Fig. 1). In the case of harbor seals, body temperature averaged 36.7±0.10 °C (n=23), which was also independent of T_a.

3.2. Seasonal changes in harp seal BMR

The rates of oxygen consumption in three male harp seals were measured 253 times throughout the study period, only 91 of which (Table 2) met the conditions for BMR.

Changes in BMR and body mass throughout the annual cycle can be observed in Fig. 4. Seasonal effects explained 32.9% of the total variation in BMR ($F_{3,83}$=25.94, P<0.0001) and differences among the three individuals accounted for 33.5% of that variation ($F_{2,83}$=26.39, P<0.0001). Variation in body mass did not have an effect on the mass-specific BMR of these three seals ($F_{1,87}$=0.26, P=0.61). The seasonal component in BMR was principally due to summer values being lower than values from all other seasons in all three males (Fig. 4). The decline in the BMR during summer was similar among the three males studied: summer BMRs were 68.4, 81.7, and 78.3% of the mean value in the three individuals for the rest of the year.

Another way of considering these seasonal variations in BMR is to compare them to a mass standard. As noted, the Kleiber (1961) curve is a high standard because the domesticated mammals used for

Table 4
Seasonal changes in body mass, energy intake, and requirements of captive seals

		Fall	Winter	Spring	Summer
Pagophilus groenlandicus					
Number of seals studied		7	7	7	8
Seasons per seal		3.2	3.2	3.4	3.7
Body mass, kg	Mean	133.6	159.2	163.8	131.7
	SE	29.44	31.05	21.91	22.17
Daily mass change, g/d	Mean	53.5	440.9	−326.5	−39.2
	SE	104.31	71.84	281.11	142.16
Maintenance energy, MJ/d	Mean	24.3	34.7	38.7	27.1
	SE	1.41	2.49	4.96	1.84
Digestible energy, MJ/d	Mean	27.0	44.2	31.1	27.4
	SE	2.61	2.72	2.70	4.09
Growth efficiency, g/MJ	Mean	38.4	62.8	60.0	28.5
	SE	5.64	35.91	14.31	8.06
Phoca vitulina					
Number of seals studied		6	6	6	6
Seasons per seal		4.9	5.0	4.6	5.7
Body mass, kg	Mean	80.6	89.6	89.8	90.3
	SE	3.03	6.36	4.22	5.79
Daily mass change, g/d	Mean	132.6	48.5	44.3	−203.3
	SE	181.12	57.67	31.84	137.67
Maintenance energy, MJ/d	Mean	29.3	22.2	19.1	22.5
	SE	5.07	6.63	5.96	4.40
Digestible energy, MJ/d	Mean	31.3	25.2	22.9	21.4
	SE	2.67	4.31	4.31	2.87
Growth efficiency, g/MJ	Mean	94.5	4.3	205.2	13.1
	SE	138.00	49.96	490.82	42.83
Pusa hispida					
Number of seals studied		2	2	2	2
Seasons per seal		2.0	2.0	2.0	2.5
Body mass, kg	Mean	44.8	46.7	46.5	42.8
	SE	4.25	5.28	0.92	1.01
Daily mass change, g/d	Mean	16.4	0.6	29.8	−34.6
	SE	20.64	14.61	10.89	89.18
Maintenance energy, MJ/d	Mean	11.8	13.5	13.8	11.7
	SE	0.24			
Digestible energy, MJ/d	Mean	13.1	12.6	15.2	11.1
	SE	1.05	0.09	0.46	3.02
Growth efficiency, g/MJ	Mean	39.8	39.8	49.3	59.2
	SE	5.79			

Individual means were weighed by the number of observations taken from each individual.

his curve had been selected for high production rates, which require high BMRs (McNab, 1980). A much more realistic standard is an all-mammal curve, such as the one described by McNab (2008), which was derived from 639 wild species. When thermoneutral measurements in harp seals are pooled over seasons to estimate individual BMRs, the mean of seven individuals was 1.82 times the all-mammal standard (Fig. 1). However, when BMR is estimated as the mean of the three individuals that were measured throughout the year, it was 1.46 times the all-mammal standard (Table 2). But, as we have seen here, basal rates are especially low in summer (Fig. 4), when the mean from the three individuals equals 1.17 times the all-mammal standard (Fig. 4). In winter the mean of the three individuals is 1.39 times and in fall 1.66 times the all-mammal standard, although one of the three individuals, TYL, had lower basal metabolic rates in all seasons (Table 2), but still higher than the all-mammal standard.

3.3. Body composition

Adult harp seal body composition was, on average, 43.6±2.26% water, 37.9±3.22% fat, and 15.9±0.83% protein, with an equivalent energy density of 18.5±1.06 MJ/kg (Table 3). Although body fat increased with body mass ($F_{1,15}=49.19$, $P\le0.0001$), the proportion of body fat did not change in relation to body mass ($F_{1,15}=3.3$, $P=0.093$). Variation in body composition was not associated with season ($F_{3,14}=3.08$, $P=0.090$), but did correlate with “seal” ($F_{3,14}=10.73$, $P=0.0035$), i.e., with individuals.

Changes in body mass were a product of changes in fat depots and lean body mass. Body mass in harp seals usually was maximal during winter, both because of an increase in lean body mass and in fat deposits, whereas the smallest total masses, lean masses, and fat deposits were usually found in summer (Table 3).

3.4. Seasonal changes in energy expenditure and food consumption

Seasonal variations in body mass, maintenance energy intake, digestible energy, and growth efficiency in 8 harp seals, 6 harbor seals, and 2 ringed seals are summarized in Table 4.

Harp seals: Although 63.7% of the variation in body mass was due to inter-individual variation, and only 10.2% was due to seasonal effects, seasonal effects were highly significant ($F_{3,90}=13.6$, $P<0.0001$) (Fig. 5). Individual differences in the rate of daily mass change were not significant ($F_{7,89}=0.7$, $P=0.70$), and season explained most (31.2%) of its variation ($F_{3,89}=14.3$, $P<0.0001$). Body mass did not have an effect on the rate of mass change ($F_{1.90}=3.2$, $P=0.08$). Food intake varied from a minimum during the fall to a maximum in winter, with a mean of 32.2±3.06 MJ/d. Individual seals had similar levels of food intake, and season was the only significant factor in the model, explaining 29% of the total variation ($F_{3,89}=15.0$, $P<0.0001$). The analysis of the relationship between daily mass change and energy intake revealed that harp seals in captivity changed their level of energy expenditure throughout the year. Maintenance requirements were lowest during fall and highest during spring, with a mean value of 31.3±2.96 MJ/d (Fig. 5). Individual seals had similar maintenance requirements with 20.4% of the overall variation due to season ($F_{3,47}=5.3$, $P<0.0031$). Body mass had no effect on maintenance requirements ($F_{1,47}=0.1$, $P=0.81$).

Harbor seals: Body mass of harbor seals varied from a maximum in summer to a minimum during the fall. The influence of season on body mass of harbor seals was significant ($F_{3,113}=11.3$, $P<0.0001$) explaining 18.5% of the total variation. Individual differences were also significant ($F_{5,113}=7.7$, $P<0.0001$) and accounted for 20.9% of the total variation in body mass. Season had an effect on the rate of daily mass change ($F_{3,112}=11.9$, $P<0.0001$) accounting for 23.3% of the total variation, whereas individual differences and body mass effects were not significant ($F_{5,112}=0.67$, $P=0.63$; $F_{1,112}=2.1$, $P=0.15$, respectively). Food intake of harbor seals was maximal during the fall, declining thereafter until summer. Season explained 20.6% of the total variation in the rate of feeding ($F_{3,112}=11.7$, $P<0.0001$), and individual differences explained 8.6% ($F_{5,112}=2.9$, $P<0.020$). Body mass had no influence on feeding rates ($F_{1,46}=1.8$, $P=0.18$). We found that harbor seals displayed seasonal changes in their level of energy expenditure. Season explained 10.6% of the total variation in maintenance requirements ($F_{3,46}=3.3$, $P<0.030$). Individual differences accounted for 23.7% of the total variation ($F_{5,46}=4.4$, $P<0.003$), whereas body mass effects were not significant ($F_{1,46}=1.8$, $P=0.18$).

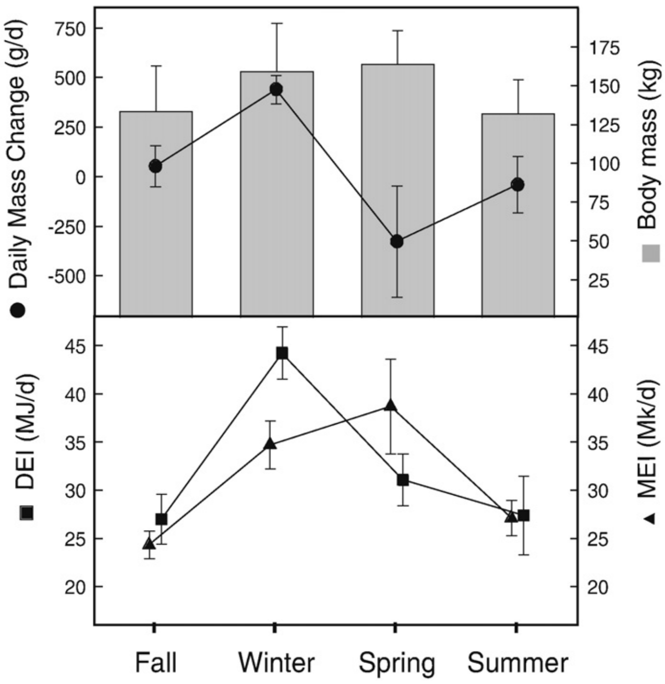

Fig. 5. Body mass, daily mass change, maintenance energy intake, and digestible energy intake as a function of season in seven harp seals, six harbor seals, and two ringed seals.

Ringed seals: The two ringed seals studied did not display seasonal changes in body mass ($F_{3,13}=1.0$, $P=0.44$). Individual differences were also not significant ($F_{1,13}=2.2$, $P=0.16$). The rate of daily mass change was not influenced by individual differences ($F_{1,12}=4.1$, $P=0.06$), season ($F_{3,12}=1.6$, $P=0.25$), or body mass ($F_{1,13}=1.1$, $P=0.32$). Ringed seals had maximal levels of food intake during spring and minimal during summer. Season explained 45.6% of the total variation in food intake ($F_{3,12}=4.7$, $P<0.03$). Individual differences explained 18.5% of the variation in feeding rates ($F_{1,12}=5.8$, $P<0.035$) and body mass explained 22.5% ($F_{1,12}=7.0$, $P<0.03$). We found that energy expenditure of ringed seals was not influenced by season ($F_{3,3}=0.7$, $P=0.60$), individual differences ($F_{1,3}=0.6$, $P=0.48$), or body mass ($F_{1,3}=2.0$, $P=0.25$).

4. Discussion

4.1. Basal rates of phocids

The thermoneutral zone in air of the harp seal was between −12 and 15 °C (Fig. 1), between 5 and 25 °C in harbor seals (Fig. 2), and at least −5 to 5 °C in the ringed seal (Fig. 2). Irving and Hart (1957) found that young harbor seals did not increase rates at air temperatures between −10 and 30 °C, but they did when in water at temperatures <10 °C. Hansen et al. (1995) reported that juvenile harbor seals increased their rates at air temperatures<−2.3 °C and >25 °C, a range similar to what we report here. Rates for an adult harbor seal have been reported constant from 20 to 35 °C with an increase in rectal

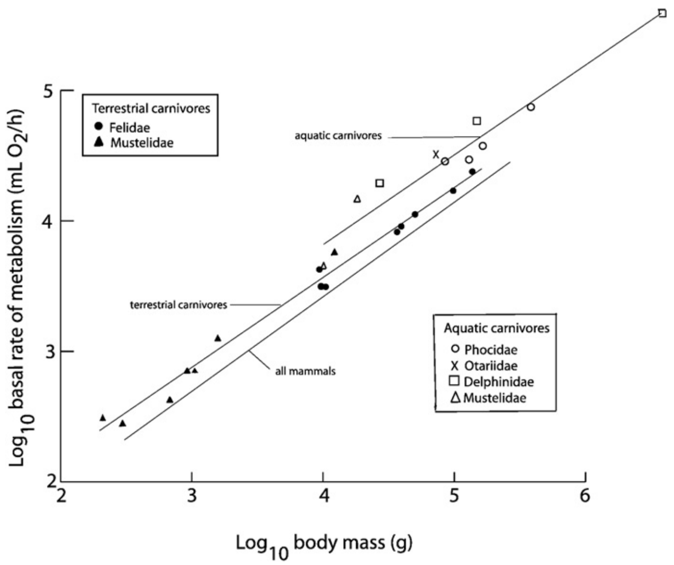

Fig. 6. Log_{10} BMR in eutherian carnivores as a function of $\log_{10}$ body mass. Curves are indicated for aquatic carnivores, terrestrial carnivores, and an all-mammal curve (McNab, 1988a,b). Data were obtained from Kanwisher and Sundnes (1965), McNab (2000, 2008), Boily and Lavigne (1997), and Williams et al. (2001).

temperature at T_as > 30 °C (Matsuura and Whittow, 1973). Geographic variation in this widely distributed species may account for some of these differences. Harp seals, however, are larger and have a more arctic distribution than harbor seals, two factors that may explain why harp seals can withstand lower ambient temperatures without increasing rate of metabolism and why their rates increased at T_as > 15 °C. Harp seals haul out on pack ice when air temperatures are low and avoid hauling out at high air temperatures (Moulton et al., 2000). Large northern elephant seals (*Mirounga angustirostris*) pups, which weighed between 60 and 110 kg and resided in cool California coastal waters, had a thermoneutral zone in water down at least to 1 °C (Noren, 2002).

Measurements of basal rate in the harp seal were made at all times of the year, all of which were used to estimate its BMR. Consequently, an appreciable variation in the basal rate remains unaccounted for by body mass (Fig. 3), some of which correlates with body composition and season. In contrast, most of the measurements made in harbor seals and in the ringed seal were made in winter.

The results reported here confirm that BMRs in phocids (Costa and Williams, 1999; Costa, 2001; Williams et al., 2001; Boyd, 2002), and specifically in the three species studied here, are higher than values predicted by the all-mammal curve (McNab, 2008). A recent study of grey seals found BMRs to be 10 to 50% higher than those predicted by mass using Kleiber's relationship (Boily and Lavigne, 1997) and 47 to 112% higher using the all-mammal curve, although, as seen here, measurements made at different times of the year can provide different estimates of BMR (Boily and Lavigne, 1997). These data generally agree with information on basal rates obtained from other phocid seal species (Fig. 6); discrepancies in the data of Parsons (1977) likely resulted from procedural peculiarities (Ochoa-Acuña, 1999).

High rates of metabolism in pinnipeds may not be simply related to aquatic habits, as was suggested by Irving (1969) and Schmidt-Nielsen (1983), but also to their food habits (Williams et al., 2001). Strictly carnivorous terrestrial mammals, like felids, also have basal rates that are higher than predicted by mass alone (McNab, 2000). In a compilation of 24 mammalian carnivores, including five phocids, two dolphins, the orca (*Orcinus orca*), one sea lion, seven mustelids (two of which are aquatic), and eight felids, BMR correlated with $\log_{10}$ body mass ($F_{1,22} = 580.00$, $P < 0.0001$); $r^2 = 0.963$:

$$\dot{V}_{O_2}(\text{mLO}_2/\text{h}) = 3.85g^{0.767}. \tag{2}$$

Basal rate in these carnivores also correlated both with $\log_{10}$ body mass ($F_{1,21} = 699.14$, $P \leq 0.0001$) and substrate ($F_{1,21} = 26.23$, $P \leq 0.0001$); $r^2 = 0.984$ (Fig. 6). Then,

$$\dot{V}_{O_2}(\text{mL/h}) = 6.27(S)g^{0.692}, \tag{3}$$

where S is a non-dimensional coefficient equal to 1.00 in terrestrial species and 1.82 in aquatic species. That is, the BMR of aquatic carnivores average 82% greater than terrestrial carnivores, which in turn have basal rates that are approximately 1.8 times those of the general mammal curve (Fig. 6), i.e., marine carnivores have BMRs that are about $(1.8)^2 = 3.3$ times those expected from mammals generally. The limited data on marine mammals appears to indicate that phocids have lower BMRs than delphinids and otariids (Fig. 6). This conclusion is justified when all 10 marine species, one mustelid, one otariid, two delphinids, one phocoenid, and five phocids, are compared: phocids had lower basal rates than a combination of the other marine mammals ($F_{1,7} = 7.94$, $P = 0.026$). Then, phocids had BMRs that were 70% of other marine carnivores: phocids therefore have BMRs that are intermediate to those of terrestrial carnivores and delphinids, otariids, and *Enhydra*.

The high BMRs found in pinnipeds therefore appear to be associated both with cold-water temperatures and carnivorous habits.

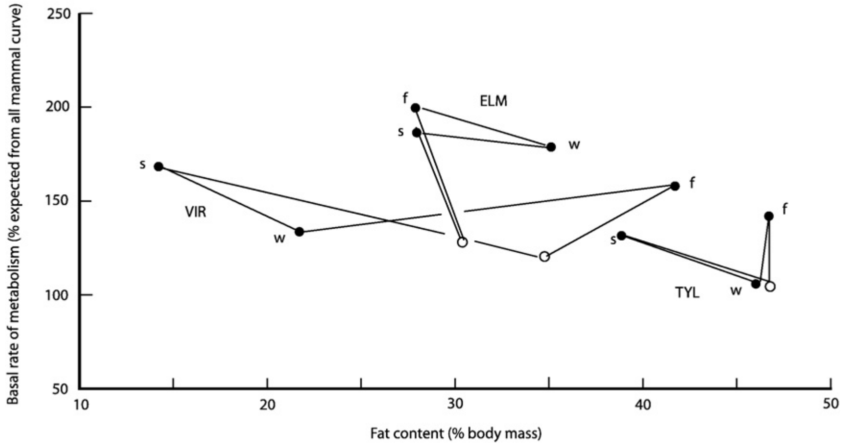

Fig. 7. Basal rate of metabolism (expressed as a % of the value expected from mass, McNab, 2008) as a function of the fat content of the body of three harp seals at four times of the year, spring (s), summer (O), fall (f), and winter (w).

Evidence of this is found in the observation that of two aquatic mustelids, the sea otter *Enhydra lutrus*, which is more aquatically specialized and has exclusively marine habits, has a higher BMR (2.08 times the values expected from Eq. (2)) than *Lutra lutra*, which has a typically carnivore BMR (1.00 times the values expected from Eq. (2)) and less committed to an aquatic existence: a similar difference (1.99:1) occurs between marine and freshwater or terrestrial mammals (McNab, 2008). The suggestion that cold-water and carnivorous habits are responsible for high BMRs in cold-water phocids and *Enhydra* can be tested by determining the BMR of warm-water counterparts, the subtropical to tropical monk seals (*Monachus*) of the Mediterranean and Hawaii, and the freshwater giant otter *Pteronura brasiliensis* of South America. We suggest that monk seals and the giant otter will have high BMRs in association with carnivory, but somewhat lower than cold-water phocids or *Enhydra*, because of their warm-water distributions.

4.2. Seasonal variations in BMR

This study demonstrated that harp seals displayed profound seasonal changes in body composition and rates of metabolism, even under conditions of captivity, which suggests that these changes might be entrained to photoperiod. Although most of the energy mobilized during periods of reduced food intake is derived from fat depots, a proportion involved changes in the lean portion of the body. Indeed, percent body fat did not change in northern elephant seal pups during the 2 to 3 month postweaning fast (Adams and Costa, 1993; Noren et al., 2003). The various body components were metabolized in proportion to their abundance, although protein catabolism accounted for only 4% of energy expenditure (Pernia et al., 1980; Rea and Costa, 1992).

Studies of changes in body composition are of great importance for elucidating how energy expenditure varies throughout the year because organs and tissues have distinctive rates of energy use. A differential reduction in the size of organs or tissues, therefore, may change the level of energy expenditure beyond that explained solely by changes in body mass. A major contributor to BMR is the respiration of organs involved in nutrient and energy processing, including the alimentary tract, liver, and kidneys (Johnson et al., 1990; Konarzewski and Diamond, 1995; Speakman and McQueenie, 1996). The correlation of BMR with organ size may permit the basal rate to change in response to the amount of nutrient and energy that needs to be processed. In this respect, BMR was found to correlate with energy assimilation rate (Daan et al., 1989; Konarzewski and Diamond, 1994).

On the other hand, considerable controversy exists regarding the relative contribution of adipose tissue to BMR. Whereas some studies suggest that fat tissue does not contribute much to total metabolism (Felig et al., 1983; Lavigne et al., 1986; Blaxter, 1989; Segal et al., 1989; Rea and Costa, 1992), other studies involving rodents (McNab, 1968; McCracken and McNiven, 1983) and sheep (McNiven, 1984) have found that fat tissue does contributes to overall metabolism. In that context, it is possible that a seasonal variation in the size of the fat deposits could account for the seasonal variation in BMR because of the presumptively low rate of metabolism of fat deposits. However, BMR, expressed relative to the values expected from total mass, is independent of the size of fat deposits, at least within individuals (Fig. 7).

The demonstration of lower levels of BMR during summer is at odds with previous research conducted by the late Dr. Renouf and her collaborators on harp seals housed at the Ocean Sciences Centre. They found that, contrary to predictions based on thermoregulation and reproduction, harp seals had higher BMRs in summer than during the rest of the year (Renouf and Gales, 1994). At least two factors may explain this disagreement. First, their study measured oxygen consumption throughout a 24-hour cycle of seals kept in a tank fitted with a Plexiglas bubble from which air samples were drawn. Seals were free to swim inside the tank during that time. To control for the effect of physical activity on oxygen consumption, these authors chose the hour with the lowest oxygen consumption as a measure of basal rate. The minimal activity in a 24-hour period of a male seal near the breeding season (especially if sexually mature females are nearby) might be higher than that of a resting seal. Another, perhaps more important, drawback of the previous study is that the design was not balanced. Single 24-hour measurements were made at various intervals, from two weeks to two months. So, some individuals were only measured twice in an entire season.

Here we explicitly avoided the complications of allowing animals free movement during the determination of the rate of oxygen consumption. A "dry" metabolic chamber in which the animal laid down during measurements was used. In addition, rates were measured in every seal more than 10 times each season, and the period between seasonal measurements was kept constant (60 days).

We believe that the results presented here accurately reflect the changes in BMR experienced by harp seals in captivity and in the wild. Our results agree with what would be expected of mammals exposed to varying levels of food intake and energy balance. During spring

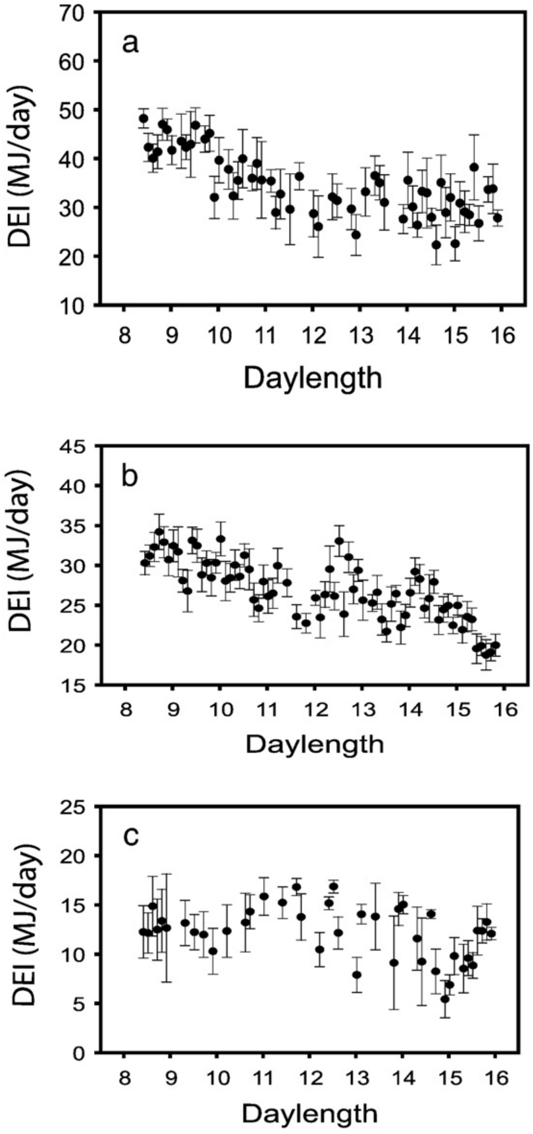

Fig. 8. Food intake as a function of photoperiod in a) seven harp seals, b) six harbor seals, and c) two ringed seals.

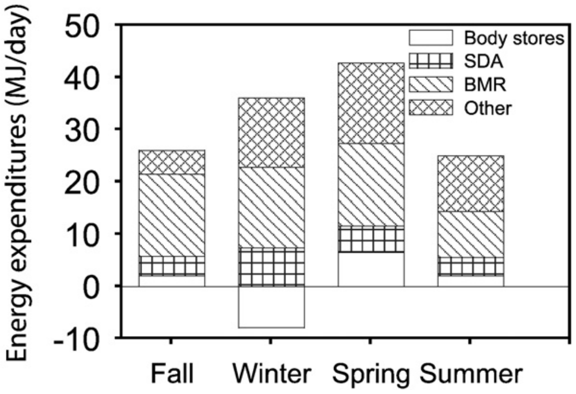

Fig. 9. Components of the daily energy budget of captive harp seals as a function of season.

and summer, although energy expenditure is relatively high, food consumption is not, which results in a negative energy balance (and body mass loss). As expected, basal rates are lower during this phase of the annual cycle, which probably slows the rate of body mass loss during this period. In addition, as food consumption is low, visceral organs probably recess in size and/or metabolic activity, as compared with periods of intense feeding during the fall when the lean mass and body fat increase in size. Such a regression may be the immediate cause for the decrease in BMR (Daan et al., 1989).

Although a tendency exists for BMR in endotherms to be considered a constant standard of performance, Kendeigh et al. (1977) demonstrated in birds that polar and temperate species often have a seasonal variation in BMR, and the lowest rate usually is in summer, a variation also seen in marine birds (Ellis and Gabrielsen, 2002). This pattern corresponds to that seen here in harp seals. That is, harp seals have their lowest basal rates, and presumably their lowest field expenditures in summer when they reside above the Arctic Circle, and markedly increase basal rate during the fall (in preparation for winter and reproduction), and have intermediate rates in winter. A recent study has also shown that captive grey seals have a similar pattern of seasonal changes in BMR (Boily and Lavigne, 1997). In that study, basal metabolic rates during the summer were found to be up to 50% lower than in the other seasons in the three females studied. Basal rate of metabolism is not an invariant characteristic of a species, but is a statistic that is sensitive at least to season and potentially to various factors that correlate with season, such as food availability (Ellis and Gabrielsen, 2002).

4.3. Seasonality in food consumption and energy expenditure

The spatial separation between feeding and breeding grounds, and the high degree of synchrony of breeding events, may have favored the development of internal circannual rhythms of food intake among phocids. Animals tend to have lower levels of energy expenditure when food consumption is low or null (e.g., Grande et al., 1958; Felig et al., 1983; Elliott et al., 1989). The depression of metabolism may be explained by the recession of organs that are involved with food processing and have a high metabolic intensity (Burrinet al., 1988; Daan et al., 1989; Burrin et al., 1990; Konarzewski and Diamond, 1995). Thus, phocids may concentrate feeding during only some periods of the year, and reduce food consumption when other activities interfere, a behavioral pattern that is facilitated by a large mass, which may explain why the annual variation in mass was 1.24:1 in harp seals, 1.12:1 in harbor seals, and 1.09:1 in ringed seals, i.e., in a sequence correlated with body mass.

Behaviors that may interfere with food consumption in phocids in particular, and mammals in general, include the necessity to devote significant amounts of time to search for mates, defend territories, chase competitors, and nurse pups during seasonally synchronized breeding events (Mrosovsky and Sherry, 1980). Renouf et al. (1988) observed a negative correlation between the number of social interactions and the rate of food intake in a group of captive harbor seals. Korhonen and Harri (1986) found that food intake and activity of farmed polecats (*Mustela putorius*) varied inversely during the year.

The cyclic anorexia in northern phocids suggests that they rely on environmental cues other than food availability to regulate food intake. Harp seals decreased food intake with increasing photoperiod during spring and summer (Fig. 8a), as did harbor seals (Fig. 8b). No clear trend between photoperiod and food intake was observed in the two ringed seals (Fig. 8c). Harp seals in the wild experience an exaggerated pattern of change of day length throughout the year compared to that experienced by the captive seals studied, although those experienced by both groups were not different during the periods of the year in which photoperiod had an effect on food intake (spring and summer).

We have demonstrated that up to 40% of the variability in energy expenditure was related to seasonal effects. Given that a major component of the energy expenditure of endotherms is BMR (Fig. 9), it is not surprising that basal rates of metabolism of harp seals change throughout the annual cycle: the low summer food intake (Fig. 8a) coincides with the lowest basal rate (Figs. 4 and 9), both because of a small mass and independently of body size.

4.4. Implications for modeling energy consumption in wild populations of pinnipeds

These results show the importance of incorporating temporal patterns into models that attempt to estimate fish consumption by populations of wild pinnipeds. This requirement is especially important for migratory species, such as the harp seal, which occupies areas involved in commercial fisheries only during fall and winter. If a model maintains energy requirements as a fixed multiple of a single BMR estimate, and therefore assumes that per capita consumption is constant over the year, it would have to assume that the population doubles from summer to winter to reflect accurately the temporal distribution of fish consumption by the harp seal herd.

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