

## INSULATION AND THERMAL BALANCE OF FASTING HARP AND GREY SEAL PUPS

GRAHAM A. J. WORTHY\*

Department of Zoology, University of Guelph, Guelph, Ontario, Canada N1G 2W1

(Received 22 March 1991)

**Abstract**—1. Harp and grey seal pups were examined during the post-weaning period to quantify their thermoregulatory abilities and thermal limits.

2. Deep body temperatures of harp seals ( $37.8 \pm 0.8^\circ\text{C}$ ) were not significantly different from those of grey seals ( $38.9 \pm 0.4^\circ\text{C}$ ).

3. As blubber depth declined during the fast, temperature gradients extended increasingly deeper into the muscle layer potentially decreasing heat loss.

4. Blubber conductivity ( $\approx 0.18 \text{ W/m}^\circ\text{C}$ ) did not vary regionally within an animal, or between animals or species.

5. Calculated lethal cold limits in air were between  $-85.4^\circ\text{C}$  and  $-116.1^\circ\text{C}$ , suggesting that fasting, weaned pups can easily cope with temperatures they would normally experience.

### INTRODUCTION

While phocid seals (Pinnipedia: Phocidae) can apparently cope with the cooling effects of the aquatic environment without a major increase in basal metabolism (Lavigne *et al.*, 1986), there may be a minimum depth of blubber which is necessary to provide adequate insulation (Drescher 1980). This is an important consideration for a group of mammals which annually undergoes prolonged fasts, during which energy for maintenance is obtained from the insulative blubber layer (Bryden, 1969; Ortiz *et al.*, 1978; Pernia *et al.*, 1980; Worthy and Lavigne, 1983, 1987). Young-of-the-year, undergoing their post-weaning fast, may be most susceptible to thermoregulatory problems. Fasting harp, *Phoca groenlandica*, and grey, *Halichoerus grypus*, seal pups may not feed for up to 8–10 weeks after weaning and may lose up to 50% of their weaning mass during this time (Brodie and Pásche, 1982; Fedak and Anderson, 1982; Worthy and Lavigne, 1983; Stewart and Lavigne, 1984; ).

During prolonged fasting, some species undergo metabolic changes which promote energy conservation. These changes may involve a drop in resting metabolic rate (e.g. Grande *et al.*, 1958; Westerterp, 1977; Øritsland *et al.*, 1985; Markussen and Øritsland, 1986; Nordøy *et al.*, 1990), a decline in the set point body temperature (e.g. Westerterp, 1977; Webb *et al.*, 1980) or a reduction in the proportion of the body maintained at deep body temperature (e.g. Aschoff and Wever, 1958). Worthy and Lavigne (1987) have shown that resting metabolic rate does not decline significantly during the post-weaning fast of either harp or grey seals, leaving the possibility

that these seals may conserve metabolic energy by other means.

The purpose of the present study was to document changes in peripheral heat exchange that may occur during the post-weaning fast of young harp and grey seals. In order to monitor their ability to maintain thermal balance during an 8–10 week fast, data were collected on deep body and surface temperatures, thermal gradients and conductance characteristics of the blubber. These data were then used in the calculation of heat losses and compared with measures of heat production obtained from indirect calorimetry.

### MATERIALS AND METHODS

Recently weaned harp (greycoat and ragged-jacket, Kovacs and Lavigne, 1985) ( $N = 12$ ) and grey seal (stage IV, Kovacs and Lavigne, 1986) ( $N = 11$ ) pups were collected from their respective breeding areas in eastern Canada and taken to Guelph, ON. Animals were kept in outdoor facilities for a maximum of 10 weeks and were part of a study investigating the body compositional changes and energetics of the post-weaning fast (Worthy, 1987; Worthy and Lavigne, 1987).

Deep body temperatures ( $T_b$ ) were measured using FM telemeters which were force-fed to the seals shortly after their arrival at the holding facilities (Worthy and Lavigne, 1987). Surface temperatures ( $T_s$ ) were collected from six sites (Fig. 1) on seals that were either in or out of the water,

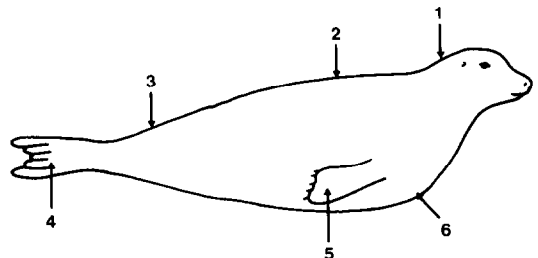


Fig. 1. Sites at which surface temperatures were measured.

\*Present address: Marine Mammal Research Program  
Departments of Marine Biology and Wildlife and Fisheries Sciences, Texas A&M University, Galveston, TX 77551, U.S.A. Telephone: (409) 740-5705; Fax: (409) 740-5717

by means of a YSI banjo temperature probe (model 409; Yellow Springs Instruments, Yellow Springs, OH) mounted on the end of a 1.5 m pole. The probe was held in place until a reading was stable for at least 30 sec. Surface temperature ( $T_s$ ) measurements in water were obtained with the animals restricted in a cage.

Ambient air temperatures ( $T_a$ ) were noted and incoming solar radiation was recorded continuously using an Eppley pyrliometer (Eppley Laboratory Inc., Newport, RI). Wind speed was determined to the nearest 0.5 m/sec using a hand held anemometer positioned 20 cm above the animal (C. F. Casella and Co. Ltd., London, U.K.).

Surface temperatures and temperature gradients in blubber and underlying muscle were determined at sites 2, 3, and 6 (Fig. 1), after the animals had been held at a  $T_a$  of  $20.1 \pm 1.1^\circ\text{C}$  ( $\pm$ SD) for 0.5 to 2.0 hr. Measurements were obtained within 5 min of the animal having been killed by a lethal dose of sodium phenobarbitol administered by a veterinarian. Temperature gradients in blubber and muscle were recorded at 1 cm increments to a total depth of 4 cm, using YSI (model 507) temperature probes mounted on the tips of 18 gauge hypodermic needles, each of which was pre-set for insertion to a fixed depth.

Sculp (blubber with skin attached) samples ( $30 \times 30$  cm) were selected from sites 1, 2 and 3 (Fig. 1) for use in heat flow measures. Hair was trimmed from all samples in order to measure the thermal characteristics of blubber and skin only, and determine potential changes in blubber/skin conductivity with age, independent of pelage differences.

Heat flow determinations were performed in a climate-controlled environmental chamber (model C810, Controlled Environment Inc., Pembina, ND) at a  $T_a$  of  $3.5 \pm 1.0^\circ\text{C}$  and a relative humidity of  $80 \pm 10\%$ . Sculp samples were placed on a steel plate box with a brass top, which was insulated on the base and all four sides and through which heated water was recirculated (Øritsland and Lavigne, 1976; Worthy 1985). This served as a heat source, maintaining a brass plate temperature of  $40.1 \pm 1.3^\circ\text{C}$ . A biomedical heat flux transducer (model HFT-A, Thermoetrics Corp. San Diego, CA) and YSI temperature probe (model 409) were placed in the center of the brass plate beneath the sample.

Measurements of heat flux ( $\text{W/m}^2$ ) and temperatures of the brass plate, skin surface ( $T_s$ ) and air ( $T_a$ ) were recorded once equilibration was attained. Blubber depth was measured directly over the site of the heat flux transducer. Conductivity ( $k$ ,  $\text{W/m}^\circ\text{C}$ ) of the blubber and skin was calculated by dividing heat flux ( $\text{W/m}^2$ ) by the temperature gradient ( $^\circ\text{C/m}$ ). Conductance ( $C$ ,  $\text{W/m}^2/^\circ\text{C}$ ) of the blubber and skin was calculated by dividing heat flux ( $\text{W/m}^2$ ) by the temperature difference ( $^\circ\text{C}$ ) between the brass plate and surface. Overall sculp conductance was estimated by combining the conductance of blubber and skin (measured above) with values for phocid pelage which had been measured either in water (Kooyman *et al.*, 1977) or in air (R. J. Hurst and N. A. Øritsland, personal communication). Heat loss (HL) was estimated using the equation:

$$\text{HL} = CA_b(T_b - T_a) \quad (1)$$

where  $C$  is overall sculp conductance ( $\text{W/m}^2/^\circ\text{C}$ ) and  $A_b$  is the measured surface area ( $\text{m}^2$ ) of the seal (Worthy, 1985; Innes *et al.*, 1990). The resulting estimates of heat loss were compared with measures of standard metabolic rate ( $R_s$ ) obtained from the same individuals by indirect calorimetry (Worthy, 1987; Worthy and Lavigne, 1987). Lethal cold limits (Bligh and Johnson, 1973) were estimated assuming a maximum metabolic rate (2.5 times  $R_s$ ) ( $\text{W/m}^2$ ) and the thermal insulation of the sculp ( $^\circ\text{C m}^2/\text{W}$ ; the inverse of conductance) to produce the maximum sustainable temperature difference between the core and the environment ( $^\circ\text{C}$ ) (Mount, 1979). The predicted cold limit is approximately equal to  $T_b$  minus the maximum temperature difference (Mount, 1979).

## RESULTS

Deep body temperatures of grey seals (mean:  $38.9 \pm 0.4^\circ\text{C}$ ,  $N = 15$ , range:  $38.7$ – $39.5^\circ\text{C}$ ;  $T_a = -5$  to  $+20^\circ\text{C}$ ) were not significantly different from those of harp seals (mean:  $37.8 \pm 0.8^\circ\text{C}$ ,  $N = 17$ ; range:  $37.0$ – $38.9^\circ\text{C}$ ;  $T_a = -6$  to  $+23^\circ\text{C}$ ) ( $P < 0.05$ ,  $t$ -test). Individual seals maintained body temperature, exhibiting little variation in  $T_b$  over the range of air and water temperatures examined despite large decreases in body mass over the duration of the post-weaning fast.

There was no significant relationship ( $P > 0.05$ ) between  $T_s$  and incoming solar radiation and/or wind speed. Surface temperatures remained above  $0^\circ\text{C}$  regardless of ambient conditions and occasionally went as high as  $38^\circ\text{C}$ , even when air temperatures were as low as  $-6^\circ\text{C}$  (Fig. 2). Surface temperature of the head (point 1) remained above  $9^\circ\text{C}$  regardless of  $T_a$ , rate of incoming solar radiation, or wind speed (Figs 2, 3, 4). Greatest variability in  $T_s$  was observed at points 2, 3 and 4 (Fig. 1) (corresponding to the mid-dorsum, tail region and hind-flipper).

Surface temperatures were less variable in water than in air and were similar to  $T_w$  over the entire range examined, with the exception of the head region (Fig. 5). Temperatures on the head always exceeded  $8^\circ\text{C}$  (Fig. 5).

There were no significant differences between individuals or species, with respect to the depth of the temperature gradient, despite large differences in the depth of the insulative blubber layer (Fig. 6). Temperature gradients resulted in temperatures of  $30$ – $35^\circ\text{C}$  at a depth of 4 cm regardless of blubber depth (Fig. 6). Gradients extended well into the underlying muscle mass when blubber depth declined (Fig. 6).

There were no significant regional differences in conductivity ( $P > 0.05$ ) within any of the individual animals, between individuals or between species. When these data were pooled, average conductivity was  $0.183 \pm 0.017 \text{ W/m}^\circ\text{C}$  (Table 1). Since there were no significant differences in conductivity measurements ( $k$ ,  $\text{W/m}^\circ\text{C}$ ) (a physical property of the tissue independent of depth) between different body regions or between individuals, the relationship for conductance ( $C$ ,  $\text{W/m}^2/^\circ\text{C}$ ), which is depth dependent, could be expressed as a function of blubber depth (BD, m) using the pooled data:

$$C = 0.44 \text{ BD}^{-0.748} \quad R^2 = 0.80. \quad (2)$$

Rates of heat loss, calculated using equations 1 and 2 were not significantly different ( $P > 0.05$ ) from values derived for the same individuals using indirect calorimetry (Worthy, 1987; Worthy and Lavigne, 1987) in either air or water. These two estimates of metabolic expenditure ( $N = 23$ ) were related by the linear regression:

$$R_s = 0.99 \text{ HL} + 0.11 \quad R^2 = 0.90. \quad (3)$$

The slope estimate does not differ significantly from unity ( $P > 0.05$ ).

Assuming a blubber depth of 4 cm and a metabolic expenditure equivalent to  $R_s$ , the estimated lower

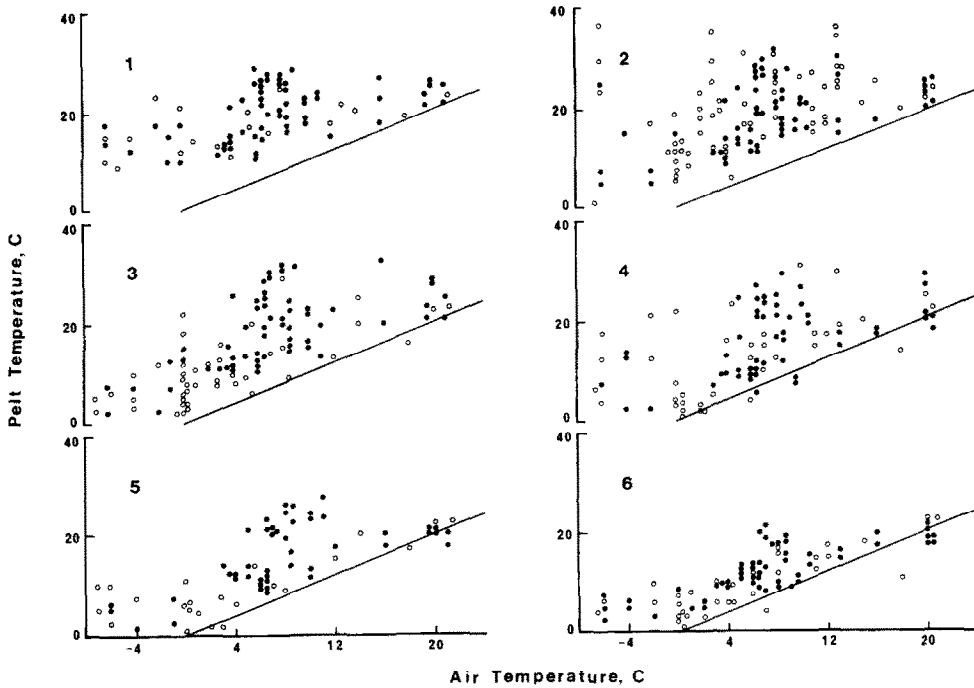


Fig. 2. Surface temperatures ( $^{\circ}\text{C}$ ) at points 1–6 (Fig. 1) as a function of air temperature ( $^{\circ}\text{C}$ ) for grey seals (open circles) and harp seals (closed circles). Lines represent equivalent surface and air temperatures.

lethal limits for weaned harp and grey seal pups were approximately  $-11.9$  and  $-23.8^{\circ}\text{C}$ , respectively (Table 2). If  $R_s$  were allowed to increase by 2.5 fold, these limits would decline to  $-85.4$  and  $-116.1^{\circ}\text{C}$ , respectively (Table 2).

#### DISCUSSION

Normally, homeotherms regulate deep body temperature within relatively narrow limits, while metabolic rate varies. There have, however, been

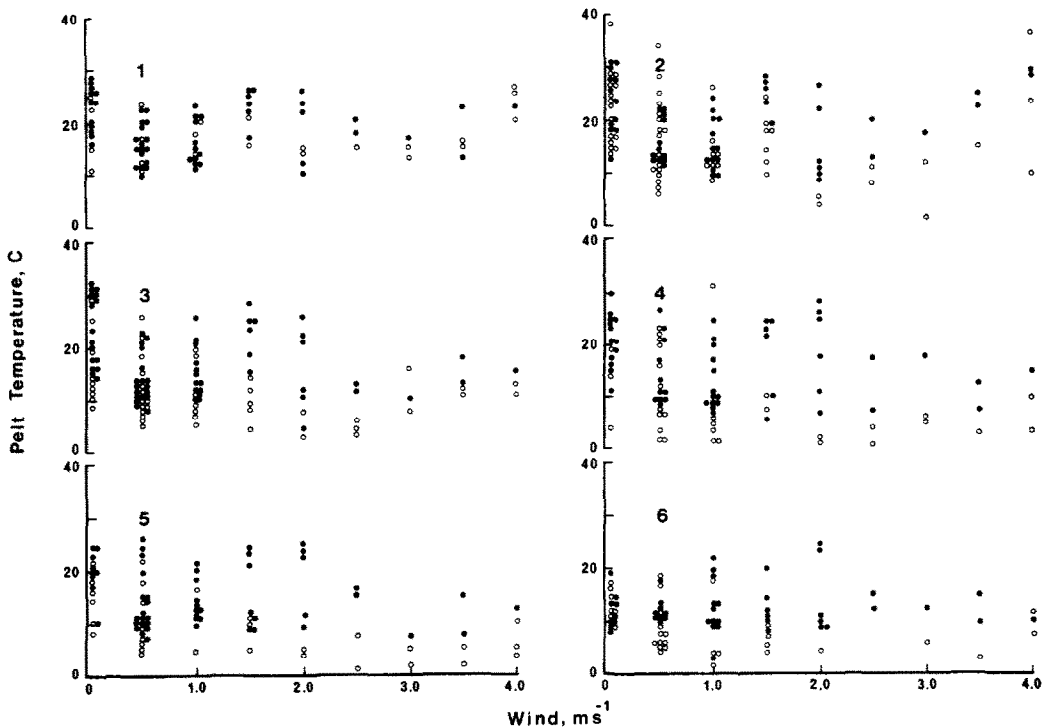


Fig. 3. Surface temperatures ( $^{\circ}\text{C}$ ) at points 1–6 (Fig. 1) as a function of wind speed (m/sec) for grey seals (open circles) and harp seals (closed circles).

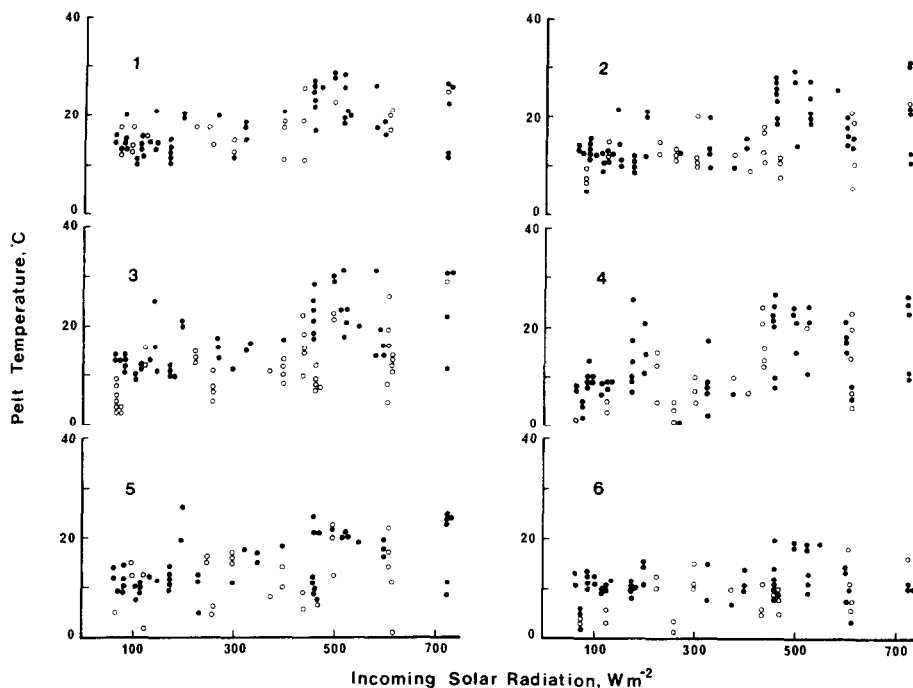


Fig. 4. Surface temperatures (°C) at points 1-6 (Fig. 1) as a function of incoming solar radiation (W/m<sup>2</sup>) for grey seals (open circles) and harp seals (closed circles).

suggestions (McGinnis and Southworth, 1971; Hampton *et al.*, 1971) that some marine mammal species may not be able to maintain body temperature unless they remain awake and/or swimming. Declines in  $T_b$  were never observed in the present study, even when long-term fasted, inactive seals were measured in water at  $\approx 2^\circ\text{C}$ .

Surface temperatures, in the present study, varied considerably. Surface temperatures approaching  $T_b$  could mean that under certain ambient conditions in air, fasting pups were deliberately losing heat to the environment via peripheral vasodilation. In water, changes in  $T_s$  mirrored those of the environment suggesting peripheral vasoconstriction. In both,

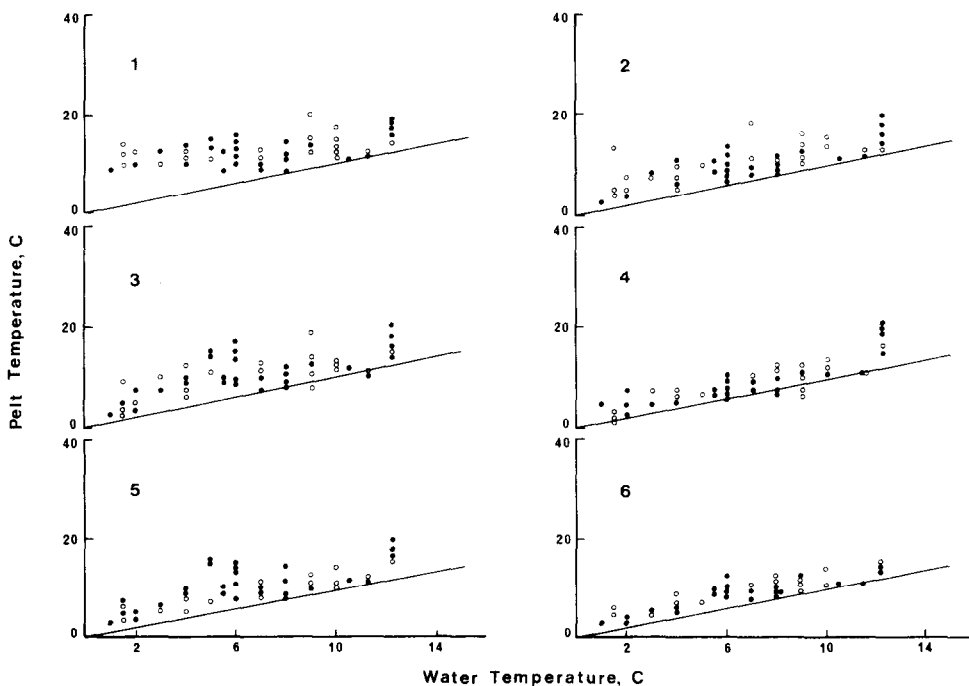


Fig. 5. Surface temperatures (°C) at points 1-6 (Fig. 1) as a function of water temperature for grey seals (open circles) and harp seals (closed circles). Lines indicate equivalent surface and water temperatures.

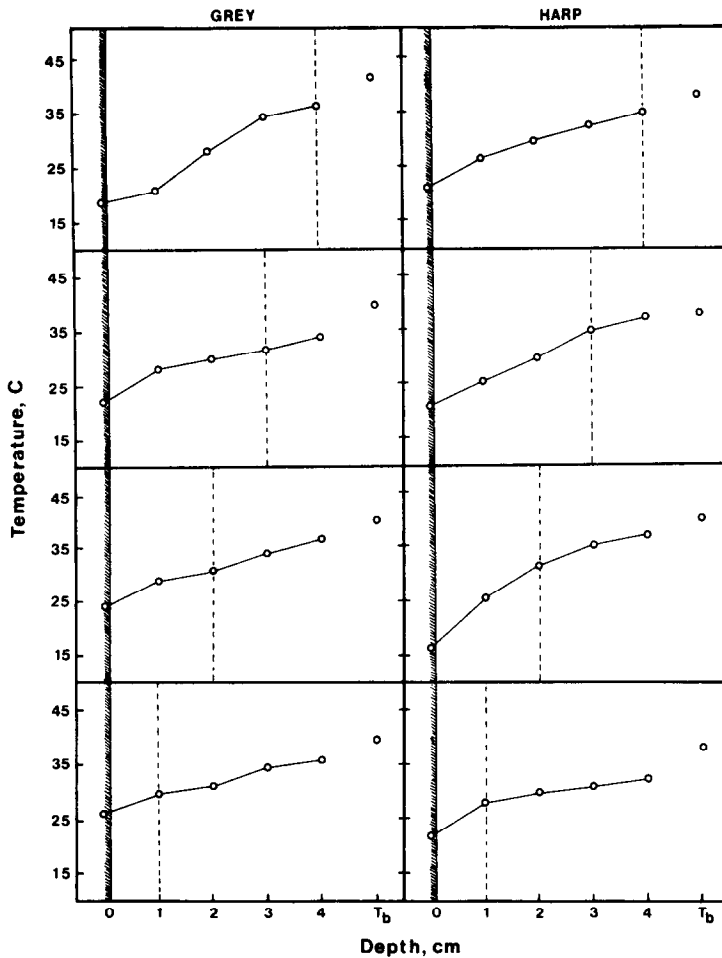


Fig. 6. Temperature gradients obtained from eight individual harp and grey seal pups with differing blubber depths (---- blubber depth, /// skin surface). Data are from seals which had been in air ( $T_a = 20 \pm 1.1^\circ\text{C}$ ) for at least 0.5 hr prior to measurement. Gradients in some instances extended well into the muscle layer when the blubber became depleted. Deep body temperature ( $T_b$ ) is shown for reference.

environments,  $T_s$  of the head was maintained at or above  $8\text{--}9^\circ\text{C}$ , indicating that the reduced depth of blubber present on the head and the maintenance of the brain at deep body temperature could result in the head region accounting for substantial heat losses at low ambient temperatures (Blix *et al.*, 1979).

Surface temperature did not show any direct relationship with wind speed, as might be predicted given the densities of phocid seal hair (approximately

$1000\text{--}2000$  hairs/ $\text{cm}^2$ ) (Scheffer, 1964). The level of wind penetrance into the pelage, and therefore its effect on surface temperature, is dependent on hair density, with  $1000$  hairs/ $\text{cm}^2$  allowing the penetration of a  $35$  km/hr wind only  $1$  or  $2$  mm into the fur (Tregear, 1965). Wind direction is also important,

Table 2. Estimated cold limits for thermoregulation in air (Mount, 1979) for a  $30$  kg harp seal and a  $45$  kg grey seal pup based on  $R_s$ , or  $2.5$  times  $R_s$ , and the thermal insulation of sculp

Metabolic rate* ( $\text{W}/\text{m}^2$ ) (A)	Thermal insulation† ( $^\circ\text{C}/\text{m}^2/\text{W}$ ) (B)	Maximum difference between core and environment ( $^\circ\text{C}$ ) ( $A \times B$ )	Predicted cold limits ( $^\circ\text{C}$ ) ( $T_b - (A \times B)$ )
Harp seal:			
128.8	0.38	48.9	$-11.9$
322.0	0.38	122.4	$-85.4$
Grey seal:			
165.2	0.38	62.8	$-23.8$
413.1	0.38	157.1	$-116.1$

\*Metabolic rate is based on either  $R_s$  or  $2.5$  times  $R_s$  (Worthy and Lavigne, 1987) expressed as a function of the estimated surface area (harp seal:  $0.59$   $\text{m}^2$ ; grey seal:  $0.61$   $\text{m}^2$ ) (Innes *et al.*, 1990).

†Thermal insulation was calculated for a blubber depth of  $4$  cm.

Table 1. Conductivities ( $\pm$ SD) of the blubber and skin for harp seal and grey seals. Values from the literature, measured under differing conditions were converted to appropriate units

Species	N	Conductivity ( $\text{W}/\text{m}^\circ\text{C}$ )
Harp seals (1)	12	$0.181 \pm 0.018$
Grey seals (1)	11	$0.184 \pm 0.025$
Mean (1)	23	$0.183 \pm 0.017$
Southern elephant seals (2) (blubber only)	2	0.071
Harbour seals (live animal) (3)	4	0.293
Harbour seals (4)	2	0.228
Ringed seal (5)	1	0.184

References: (1) present study, (2) Bryden (1964), (3) Hart and Irving (1959), (4) R. J. Hurst and N. A. Øritsland personal communication, (5) Scholander *et al.* (1942).

making it difficult to assess the overall effects of wind on coat insulation of windward and leeward surfaces, although the stiff hairs of an adult phocid would not move much and some seals do appear to orient with the wind (Ray and Fay, 1968; Ray and Smith, 1968).

To estimate heat losses across a given surface area, the thermal conductivity of the insulator and the temperature difference must be known. The temperature gradient that is maintained between environmental and internal temperatures is often assumed to be deep body temperature minus ambient temperature, maintained over the depth of the insulative blubber layer. Temperature gradients measured in the present study extended well into the muscle mass below the blubber when the insulative layer became depleted. Conversely, in times of heat stress, the blubber layer can be bypassed by peripheral vasodilation, thereby decreasing the depth of the gradient (Matsuura and Whittow, 1975). The ability to increase the depth of the temperature gradient, and thereby decrease the proportion of the body being maintained at deep body temperature, is one potential mechanism by which fasting phocids may reduce their metabolic expenditures.

Measures of conductivity obtained from fresh dead blubber should approximate maximum insulation values, i.e. maximum vasoconstriction, and therefore approximate minimum heat loss values. Measures of conductivity collected from live animals may be higher (Table 1), due to peripheral vasodilation. Conductivity measurements in the present study, indicate an absence of any significant change in the quality of insulation through the post-weaning fast. This suggests that there is neither a selective mobilization of specific lipids as energy sources during the fast nor any change in the basic composition of the blubber, contrary to what appears to be true for some cetaceans (e.g. Lockyer *et al.*, 1986; Worthy and Edwards, 1990).

Drescher (1980) suggested that 1.5 cm may be the minimum blubber depth, below which insulation is insufficient for the maintenance of homeothermy in harbour seals, *Phoca vitulina*. This suggestion is difficult to verify. Heat losses do appear to increase rapidly in weaned harp and grey seal pups at blubber depths of less than 1.5 cm (Worthy, 1985), implying that perhaps this is the lower limit for effective insulation. Ryg *et al.* (1988) have suggested that absolute depth is not the most critical factor, but rather it is the ratio between blubber depth and body radius that is critical. As long as this ratio is maintained, an animal can maintain thermal homeostasis. Ryg *et al.* (1988) suggest that this may be the reason why harp seals do not show large increases in metabolic rate during the post-weaning fast while grey seals do (Worthy and Lavigne, 1987).

An individual homeotherm's energy budget is a balance of energy input and outflow, with heat losses through evaporation, radiation, convection and conduction balancing gains via metabolic heat production and energy absorbed from incoming solar radiation (Porter and Gates, 1969). Evaporative losses can largely be ignored for phocid seals (Ling, 1974; Gallivan and Ronald, 1979), particularly over the temperature range normally experienced by these animals. If one assumes that body temperature is

constant over the long term and that there is no net loss or gain due to radiative exchange, then metabolic heat production can be estimated indirectly from convective and conductive heat losses (Mount, 1979).

The present study suggests that metabolic expenditures of young phocid seals can be adequately described using a relationship incorporating the surface area of the seal, the conductance of the sculp and the temperature gradient in blubber and muscle. These calculated estimates of heat loss are comparable to estimates of heat production obtained by indirect calorimetry. If metabolic rate is increased by 2.5-fold (Lavigne, 1982), lower lethal limits of approximately  $-85.4$  and  $-116.1^{\circ}\text{C}$ , for harp and grey seals respectively, were calculated (Mount, 1979) (Table 2). Rearranging equation (2) to solve for metabolic rate at an ambient air temperature of  $-30^{\circ}\text{C}$  (a temperature at the lower end of the normal range of ambient temperatures encountered), harp seals would expend only  $104.0\text{ W}$  (1.4 times  $R_b$ ) and grey seals only  $110.8\text{ W}$  (1.1 times  $R_b$ ). These metabolic rate values and calculated lethal limits suggest that recently weaned, fasting harp and grey seal pups can easily cope with the thermal demands placed upon them by their respective terrestrial environments with only modest increases in metabolic rate (Worthy, 1987; Worthy and Lavigne, 1987).

**Acknowledgements**—I would like to thank J. Moir, L. Piercey, R. Whitcroft, M. Wiercinski and W. Worthy for assisting in the collection of surface and body temperatures and M. Earle for his help in the measurement of thermal conductivity. Drs D. P. Costa, S. D. Feldkamp and D. M. Lavigne supplied helpful comments on the manuscript. This study was supported by an operating grant from the Natural Sciences and Engineering Research Council to D. M. Lavigne. The author was supported by a Canadian National Sportsmen's Show Fellowship, an Ontario Graduate Scholarship and a Norman James Aquatic Mammals Fellowship during the course of this research.

## REFERENCES

- Aschoff J. and Wever R. (1958) Kern und schale im Wärmehaushalt des menschen. *Naturwissenschaften* **45**, 477–485.
- Bligh J. and Johnson K. G. (1973) Glossary of terms for thermal physiology. *J. appl. Physiol.* **35**, 941–961.
- Blix A. S., Grav H. J. and Ronald K. (1979) Some aspects of temperature regulation in newborn harp seal pups. *Am. J. Physiol.* **236**, R188–R197.
- Brodie P. F. and Pásche A. J. (1982) Density dependent condition and energetics of marine mammal populations in multispecies management. *Can. Spec. Publ. Fish. Aqu. Sci.* **59**, 35–38.
- Bryden M. M. (1964) Insulating capacity of the subcutaneous fat of the southern elephant seal. *Nature* **203**, 1299–1300.
- Bryden M. M. (1969) Relative growth of the southern elephant seal, *Mirounga leonina* (L.). *Aust. J. Zool.* **17**, 153–177.
- Drescher H. E. (1980) Biology, ecology and conservation of harbour seals in the tidelands of Schleswig-Holstein. *Can. Transl. Fish. Aquat. Sci.* No. 4635.
- Fedak M. A. and Anderson S. S. (1982) The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). *J. Zool., Lond.* **198**, 473–479.

- Gallivan G. J. and Ronald K. (1979) Temperature regulation in freely diving harp seals (*Phoca groenlandica*). *Can. J. Zool.* **57**, 2256–2263.
- Grande F., Anderson J. T. and Keys A. (1958) Changes of basal metabolic rate in man in semistarvation and refeeding. *J. appl. Physiol.* **12**, 230–238.
- Hampton I. F. G., Whittow G. C., Szekerczes J. and Rutherford S. (1971) Heat transfer and body temperature in the Atlantic bottlenosed dolphin, *Tursiops truncatus*. *Int. J. Biochim. Biomet.* **15**, 247–253.
- Hart J. S. and Irving L. (1959) The energetics of harbour seals in air and in water with special consideration to seasonal changes. *Can. J. Zool.* **37**, 447–457.
- Innes S., Worthy G. A. J., Lavigne D. M. and Ronald K. (1990) Surface areas of phocid seals. *Can. J. Zool.* **68**, 2531–2538.
- Kooyman G. L., Davis R. W. and Castellini M. A. (1977) Thermal conductance of immersed pinniped and sea otter pelts before and after oiling with Prudhoe Bay crude. In *Fate and Effects of Petroleum Hydrocarbons in Marine Organisms and Ecosystems* (Edited by Wolfe D. A.), pp. 151–157. Pergamon Press, New York.
- Kovacs K. M. and Lavigne D. M. (1985) Neonatal growth and organ allometry of Northwest Atlantic harp seals (*Phoca groenlandica*). *Can. J. Zool.* **63**, 2793–2799.
- Kovacs K. M. and Lavigne D. M. (1986) Growth of grey seal (*Halichoerus grypus*) neonates: differential maternal investment in the sexes. *Can. J. Zool.* **64**, 1937–1943.
- Lavigne D. M. (1982) Pinniped thermoregulation: comments on the "Effects of cold on the evolution of pinniped breeding systems". *Evolution* **36**, 409–414.
- Lavigne D. M., Innes S., Worthy G. A. J., Kovacs K. M., Schmitz O. J. and Hickie J. P. (1986) Metabolic rates of seals and whales. *Can. J. Zool.* **64**, 279–284.
- Ling J. K. (1974) The integument of marine mammals. In *Functional Anatomy of Marine Mammals* (Edited by Harrison R. J.), Vol. 2, pp. 1–44. Academic Press, London.
- Lockyer C. H., McConnell L. C. and Waters T. D. (1986) The biochemical composition of fin whale blubber. *Can. J. Zool.* **62**, 2553–2562.
- Matsuura D. T. and Whittow G. C. (1975) Thermal insulation of the California sea lion during exposure to heat. *Comp. Biochem. Physiol.* **51A**, 757–758.
- Markussen N. H. and Øritsland N. A. (1986) Metabolic depression and heat balance in starving Wistar rats. *Comp. Biochem. Physiol.* **84A**, 771–776.
- McGinnis S. M. and Southworth T. P. (1971) Thermoregulation in the northern elephant seal, *Mirounga angustirostris*. *Comp. Biochem. Physiol.* **40A**, 893–898.
- Mount L. E. (1979) *Adaptation to Thermal Environment. Man and His Productive Animals*. University Park Press, Baltimore.
- Nordøy E. S., Ingebreetsen O. C. and Blix A. C. (1990) Depressed metabolism and low protein catabolism in fasting grey seal pups. *Acta Physiol. Scand.* **139**, 361–369.
- Øritsland N. A. and Lavigne D. M. (1976) Radiative surface temperatures of exercising polar bears. *Comp. Biochem. Physiol.* **53A**, 327–330.
- Øritsland N. A., Päsche A. J., Markussen N. H. and Ronald K. (1985) Weight loss and catabolic adaptations to starvation in grey seal pups. *Comp. Biochem. Physiol.* **82A**, 931–933.
- Ortiz C. L., Costa D. P. and Le Boeuf B. J. (1978) Water and energy flux in elephant seal pups fasting under natural conditions. *Physiol. Zool.* **51**, 166–178.
- Pernia S. D., Hill A. and Ortiz C. L. (1980) Urea turnover during prolonged fasting in the northern elephant seal. *Comp. Biochem. Physiol.* **65B**, 731–734.
- Porter W. P. and Gates D. M. (1969) Thermodynamic equilibria of animals with environment. *Ecol. Monogr.* **39**, 245–270.
- Ray C. and Fay F. H. (1968) Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus) II. Evidence from physiological characteristics. *Zoologica* **53**, 19–32.
- Ray C. and Smith M. S. R. (1968) Thermoregulation of the pup and adult Weddell seal, *Leptonychotes weddelli* (Lesson), in Antarctica. *Zoologica* **53**, 33–46.
- Ryg M., Smith T. G. and Øritsland N. A. (1988) Thermal significance of the topographical distribution of blubber in ringed seals (*Phoca hispida*). *Can. J. Fish. Aqu. Sci.* **45**, 985–992.
- Scheffer V. B. (1964) Hair patterns in seals (Pinnipedia). *J. Morph.* **115**, 291–304.
- Scholander P. F., Irving L. and Grinnell S. W. (1942) On the temperature and metabolism of the seal during diving. *J. Cell. comp. Physiol.* **19**, 67–78.
- Stewart R. E. A. and Lavigne D. M. (1984) Energy transfer and female condition in nursing harp seals, *Phoca groenlandica*. *Holarctic Ecol.* **7**, 182–194.
- Treager R. T. (1965) Hair density, wind speed and heat loss in mammals. *J. appl. Physiol.* **20**, 796–801.
- Webb G. P., Jagot S. A., Rogers P. D. and Jakobsen M. E. (1980) The effects of fasting on thermoregulation in normal and obese mice. *IRCS Med. Sci.* **8**, 163–164.
- Westerterp K. (1977) How rats economize—energy loss in starvation. *Physiol. Zool.* **50**, 331–362.
- Worthy G. A. J. (1985) Thermoregulation of young phocid seals. PhD. thesis, University of Guelph, Guelph, ON, Canada.
- Worthy G. A. J. (1987) Metabolism and growth of young harp and grey seals. *Can. J. Zool.* **65**, 1377–1382.
- Worthy G. A. J. and Lavigne D. M. (1983) Energetics of fasting and subsequent growth in weaned harp seal pups, *Phoca groenlandica*. *Can. J. Zool.* **61**, 447–456.
- Worthy G. A. J. and Lavigne D. M. (1987) Mass loss, metabolic rate and energy utilization by harp and grey seal pups during the post-weaning fast. *Physiol. Zool.* **60**, 352–364.
- Worthy G. A. J. and Edwards E. F. (1990) Morphometric and biochemical factors affecting heat loss in a small temperate cetacean (*Phocoena phocoena*) and a small tropical cetacean (*Stenella attenuata*). *Physiol. Zool.* **63**, 432–442.