



To each its own: Thermoregulatory strategy varies among neonatal polar phocids



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ABSTRACT

Cold environmental conditions and small body size promote heat loss and may create thermoregulatory challenges for marine mammals born in polar regions. However, among polar-born phocid seal species there are variations in physical attributes and environmental conditions at birth, allowing for an interesting contrast in thermoregulatory strategy. We compared thermoregulatory strategies through morphometrics, sculp attributes (conductivity and resistance), nonshivering thermogenesis (NST via uncoupling protein 1; UCP1), and muscle thermogenesis (via enzyme activity) in neonatal harp (*Pagophilus groenlandicus*), hooded (*Cystophora cristata*), and Weddell seals (*Leptonychotes weddellii*). Harp seals are the smallest at birth (9.8 ± 0.7 kg), rely on lanugo ($82.49 \pm 3.70\%$ of thermal resistance), and are capable of NST through expression of UCP1 in brown adipose tissue (BAT). In contrast, hooded seal neonates (26.8 ± 1.3 kg) have 2.06 ± 0.23 cm of blubber, accounting for $38.19 \pm 6.07\%$ of their thermal resistance. They are not capable of NST, as UCP1 is not expressed. The large Weddell seal neonates (31.5 ± 4.9 kg) rely on lanugo ($89.85 \pm 1.25\%$ of thermal resistance) like harp seals, but no evidence of BAT was found. Muscle enzyme activity was highest in Weddell seal neonates, suggesting that they rely primarily on muscle thermogenesis. Similar total thermal resistance, combined with marked differences in thermogenic capacity of NST and ST among species, strongly supports that thermoregulatory strategy in neonatal phocids is more closely tied to pups' surface area to volume ratio (SA:V) and potential for early water immersion rather than mass and ambient environmental conditions.

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1. Introduction

Thermoregulatory homeostasis can be challenging for marine mammals that live in cold and aquatic environments and is managed through a combination of behavioral and physiological mechanisms (Scholander et al., 1950; Ryg et al., 1993; Liwanag et al., 2009). Heat loss in adult marine mammals is typically reduced by lower surface area to volume ratios (SA:V) compared with terrestrial animals of similar size (Innes et al., 1990; Oftedal et al., 1991), reduced peripheral blood flow (vasoconstriction), counter-current heat exchangers (Scholander et al., 1950), and effective insulation (Scholander et al., 1950; Dunkin et al., 2005; Liwanag et al., 2012a, 2012b). A thick subcutaneous lipid depot

provides insulation in adult phocid seals (Kvadsheim and Folkow, 1997; Liwanag et al., 2012b). Their blubber layer protects against the cold and is effective against the increased conductivity of water experienced as a result of their aquatic lifestyle. In general, it is thought that adult phocid seals have broad thermal neutral zones as a result of this thick blubber layer (Hokkanen, 1990).

Unlike adult seals, which rely on blubber, most phocid seal pups are born with little or no blubber and rely instead on a lanugo coat (Scholander et al., 1950; Ling, 1974; Elsner et al., 1977; Oftedal et al., 1991; Kvadsheim and Aarseth, 2002). Phocid pup fur is lighter and more insulative in air than a similar thickness of blubber; small-bodied animals can achieve greater insulation with less volume and weight using fur compared with blubber (Ryg et al., 1993). However, when phocid fur becomes wet, water replaces the warm, trapped air in the under-fur and heat can be readily conducted away from the body (Scholander et al., 1950; Davydov and Makarova, 1964; Elsner et al., 1977; Kvadsheim and Aarseth, 2002). Accordingly, lanugo is a good insulator for phocid species that live in dry environments or on stable substrates (i.e., elephant seals, *Mirounga angustirostris* and ribbon seals, *Histiophoca fasciata*) (Oftedal et al., 1991; Smith et al., 1991). However, it is not as effective for species with high potential for early immersion

Abbreviations: BAT, brown adipose tissue; COX, cytochrome c oxidase; CS, citrate synthase; FMR, field metabolic rate; HOAD, β -hydroxyacyl CoA dehydrogenase; LD, longissimus dorsi; MR, metabolic rate; MT, mitochondria; NST, nonshivering thermogenesis; PWF, post weaning fast; SA:V, surface area to volume ratio; ST, shivering thermogenesis; UCP1, uncoupling protein 1; TEM, transmission electron microscope.

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in water, as may occur in species born on unstable pack ice, or phocid species that naturally enter the water early in life (hooded seals, *Cystophora cristata* and harbor seals, *Phoca vitulina*) (Ofteidal et al., 1991). In these species, pups molt the lanugo in utero, and are born with a subcutaneous blubber layer and a more adult-like pelage (Burns, 1970; Bowen et al., 1987; Ofteidal et al., 1991). The deposition of a sufficiently thick blubber layer in utero can provide neonates with effective insulation even if they enter the water; therefore, lanugo is extraneous (Ofteidal et al., 1991).

Neonatal phocids are precocial compared with most other terrestrial carnivores (Kovacs and Lavigne, 1986, 1985), but they are typically born without the heat conserving adaptations of adults (Scholander et al., 1950; Irving and Hart, 1957; Blix and Steen, 1979). Young phocids have a large SA:V (Blix and Steen, 1979; Ofteidal et al., 1991) and poorly developed vasocontrol (Lapierre et al., 2004). Yet somehow, they maintain a stable core body temperature (Scholander et al., 1950; Irving and Hart, 1957; Blix and Steen, 1979; Little, 1995), even when ambient temperatures are well below freezing (Ortislund and Ronald, 1978; Blix and Steen, 1979). To maintain euthermia, young seals may employ thermoregulatory strategies not used by adults to increase their thermogenic capacity. Thermogenic capacity is determined by metabolic rate (MR), NST in brown adipose tissue (BAT) (Cannon and Nedergaard, 2004), shivering thermogenesis (ST) (Davydov and Makarova, 1964; Elsner et al., 1977; Blix et al., 1979), and/or futile cycling of calcium ions in muscle (de Meis et al., 2005; Arruda et al., 2007). However, these mechanisms come at a high metabolic cost (Cannon and Nedergaard, 2004; de Meis et al., 2005), reducing the energy available for growth and development. Selective pressure may result in using these mechanisms sparingly (Thompson et al., 1987; Little, 1995).

Although neonatal mass typically scales with maternal mass (Schulz and Bowen, 2004; Wheatley et al., 2006), differences in pelage, blubber thickness, and body size are common among young phocids. For example, harp (*Pagophilus groenlandicus*) and hooded seals are born on pack ice in March when ambient air temperatures are low and storm events are common (Table 1). Yet, harp seals have a small body size (~7% of maternal mass; Table 2; Anderson and Fedak, 1987), a very thin blubber layer, and a white lanugo coat that provides the primary insulation (Kvadsheim and Aarseth, 2002; Pearson et al., 2014). Hooded seal pups are larger (typically 11% of maternal body mass; Table 2; Bowen et al., 1985; Anderson and Fedak, 1987), they molt their lanugo pelage in utero, and a blubber layer provides insulation (Bowen et al., 1985; Ofteidal et al., 1991; Lydersen et al., 1997). At the opposite pole, the larger Weddell seals (*Leptonychotes weddellii*) are born on stable fast ice in October and November around Antarctica, when severe weather and storms are common (Table 1). Though large in body mass, neonatal Weddell seals are small relative to maternal mass (~6%; Table 2; Anderson and Fedak, 1987; Wheatley et al., 2006), and they are born with little blubber and a wettable lanugo (Elsner et al., 1977). These three species each highlight a different characteristic of young phocids, which make them a good comparison.

Table 1

Environmental variables (mean \pm SD) from 2003 to 2013 for the 3 sampling locations (Gulf of St. Lawrence, Canada, "West Ice", Greenland, McMurdo Sound, Antarctica) during the peak pupping dates by location for harp, hooded, and Weddell seals.

	Gulf of St. Lawrence ¹	"West Ice" ²	McMurdo Sound ³
Species	Harp/hooded	Harp/hooded	Weddell
Birth substrate	Pack ice	Pack ice	Fast ice
Ambient temperature (°C)	-5.13 \pm 4.28	-2.80 \pm 3.84	-15.28 \pm 3.11
Minimum temperature (°C)	-7.90 \pm 4.82	-4.71 \pm 3.93	-18.99 \pm 3.41
Maximum temperature (°C)	-2.21 \pm 4.44	-1.02 \pm 3.49	-12.12 \pm 3.20
Daily precipitation (mm)	3.36 \pm 6.47	1.57 \pm 2.54	0.13 \pm 0.49
Total precipitation (mm)	30.85 \pm 15.61	15.62 \pm 11.75	2.07 \pm 1.51

¹ Data from Environment Canada: Climate (<http://climate.weather.gc.ca/>).

² Data from Norwegian Meteorological Institute (<http://met.no/English/>).

³ Data from Antarctic Meteorological Research Center, University of Wisconsin–Madison.

Table 2

Condition indices of neonatal harp, hooded, and Weddell seals (mean \pm SEM), as well as published values on maternal mass, length of nursing period, and pup growth rate. Letters in superscript indicate significant differences among mean values ($p < 0.05$) for which there was an effect of species.

	Harp seal	Hooded seal	Weddell seal
Mass [kg]	9.8 \pm 0.7 ^a	26.8 \pm 1.3 ^b	31.5 \pm 4.9 ^b
Standard length [cm]	82.8 \pm 2.8 ^a	100.7 \pm 2.2 ^b	122.2 \pm 6.2 ^c
Surface area [m ²]	325.2 \pm 13.9 ^a	616.4 \pm 39.1 ^b	572.6 \pm 32.3 ^b
Total volume [L]	11.05 \pm 0.82 ^a	34.41 \pm 3.17 ^b	21.07 \pm 2.94 ^c
SA:V	29.62 \pm 0.99 ^b	18.05 \pm 0.51 ^a	28.80 \pm 2.61 ^b
Blubber depth [cm]	0.8 \pm 0.1 ^a	2.1 \pm 0.1 ^b	0.5 \pm 0.1 ^a
% blubber by volume	13.47 \pm 1.01 ^a	34.42 \pm 1.42 ^b	9.38 \pm 1.54 ^a
Lipid droplet volume density (%)	72.36 \pm 6.22 ^a	91.03 \pm 2.16 ^a	54.40 \pm 5.75 ^b
% maternal mass at birth ¹	7%	11%	5%
Nursing period [days] ²	10–12 days	3–5 days	35–49 days
Pup growth rate [kg day ⁻¹] ³	2.3 \pm 0.11	5.9–7.1	2.0 \pm 0.10

¹ From Anderson and Fedak (1987).

² Values for harp seals: Kovacs et al. (1991); hooded seal: Lydersen et al. (1997) and Bowen et al. (1985); Weddell seals: Teadman and Bryden (1979) and Hill (1987).

³ Values for harp seals: Kovacs et al. (1991); hooded seals: Lydersen et al. (1997); Weddell seals: Hill (1987).

Previous studies on thermoregulation in young phocids primarily focused on mechanisms preventing heat loss (Scholander et al., 1950; Blix and Steen, 1979; Kvadsheim and Aarseth, 2002), with little work quantifying heat-generating mechanisms. Additionally, for a given species and age class few studies (e.g., Pearson et al., 2014) have quantified a comprehensive suite of thermoregulatory mechanisms. In this study, we used a comparative approach to quantify insulation, the capacity for NST, and muscle thermogenesis (via muscle enzyme activity) in harp, hooded, and Weddell seals. We related the primary thermoregulatory mechanism to what is known about the environmental conditions (e.g., ambient temperature and substrate stability) for each species. Further, we examined how thermoregulatory strategies differ among species with different developmental patterns. Because there are large differences in the duration of lactation and maternal energy investment among phocids (Kovacs and Lavigne, 1986; Boness and Bowen, 1996; Ofteidal et al., 1996; Schulz and Bowen, 2004), we compared neonatal pups at an equivalent developmental stage (Kovacs and Lavigne, 1986). We hypothesized that harp seals may rely on thermogenesis via NST or muscle thermogenesis to maintain euthermia at birth (Davydov and Makarova, 1964; Blix et al., 1979; Kvadsheim and Aarseth, 2002), and hooded seal neonates may not require additional thermogenesis, as their smaller SA:V and blubber make them better insulated. We hypothesized that Weddell seals may also rely on thermogenesis via NST or muscle thermogenesis to maintain euthermia, as they are born into a harsher environment with very little blubber.

2. Materials and methods

2.1. Sample collection

Ten harp seal (*P. groenlandicus*) neonates (within hours of birth; 6 from Canada, 4 from Greenland; 5 males, 5 females) and 8 hooded seal (*C. cristata*) neonates (within hours of birth; 5 from Canada, 3 from Greenland; 5 males, 3 females) were captured in March 2008 in the Gulf of St. Lawrence, Canada (N47°36' W62°13'), and in March 2011 in the "West Ice" off Greenland (N72°24', W14°15'). Harp and hooded seal pups were aged based on coat appearance and mass (Stewart and Lavigne, 1980; Bowen et al., 1987). Pups were sacrificed using methods approved for scientific harvest in Canada (DFO Permit: IML-2007-04) or Norway (Directorate of Fisheries under the Norwegian Ministry of Fisheries and Coastal Affairs #7764 4900). Six frozen Weddell seal (*L. weddellii*) neonate carcasses (3 males, 3 females) were opportunistically collected in October 2010 and 2011 from the McMurdo Sound region (S77°40', E166°30'). All pups were less than 2 days old as determined by the presence of the placental sac ($n = 3$), freshness of the umbilicus ($n = 1$), or

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