From ice to ocean: changes in the thermal function of harp seal pelt with ontogeny

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Abstract

Many animals exhibit ontogenetic changes associated with adaptations for survival. Harp seals (Pagophilus groenlandicus) live in the Arctic and rely on thick insulation to maintain thermal homeostasis. Adult harp seals primarily use blubber for insulation, but newborn harp seals rely on a lanugo pelt while nursing, as their blubber layer develops and their first-year pelage grows. This study compared ontogenetic changes in the thermal properties of harp seal pelts in water and in air. Thermal conductivity, pelt thickness, and thermal resistance were measured in water for pelts of harp seal neonates (1 day old), thin whitecoats (4 day old), fat whitecoats (9 day old), ragged jackets (2 week old), beaters (3 week old), and adults and compared to previously published measurements made on the same pelts in air. Pelt conductivity was significantly higher in water than air for pre-molt and molting pups (P ≤ 0.031). Unlike adult pelage, which flattened underwater, lanugo hairs lifted underwater, a phenomenon that has not been reported previously. Thermal resistance of the pelt was significantly reduced in water compared to air for neonates and thin whitecoats (P ≤ 0.0001). A mathematical model of conductive heat transfer for an ellipsoid body showed volume-specific heat loss in water decreased and then stabilized as harp seals aged (P = 0.0321) and was significantly higher for neonates, thin whitecoats, and ragged jackets in water than in air (P ≤ 0.0089). Overall, pelt function is reduced in water for harp seal pups with lanugo, and this renders neonates and thin whitecoats particularly vulnerable to heat loss if submerged.

Keywords Thermoregulation · Insulation · Lanugo · Blubber · Development

Introduction

Developmental changes in physiology are frequently exhibited among animals as an adaptive response for survival in their environment. Some of these ontogenetic changes manifest in body size and muscle growth (Choi et al. 1993), locomotor performance (Carrier 1983, 1996; Garland 1985), oxygen storage capacity (Burns et al. 2007; Kanatous et al. 2008), cardiovascular capabilities (Lapierre et al. 2004; Greaves et al. 2005), metabolism (Garland and Else 1987; Thometz et al. 2014), and thermoregulatory capability (Hansen and Lavigne 1997; Donohue et al. 2000; Déglétagne et al. 2013). Although phenology varies with species, ontogenetic changes are imperative as immature animals are often more vulnerable to predation and environmental stressors.

The harp seal (Pagophilus groenlandicus) is a phocid (true seal) species that lives in the North Atlantic and Arctic Oceans and thus requires an efficient form of insulation to maintain core body temperature. Harp seals transition from a terrestrial lifestyle to a more aquatic one in their early life (Kovacs and Lavigne 1986; Burns et al. 2007). Neonates are born on pack ice with a thick lanugo coat and a thin blubber layer (Lavigne and Kovacs 1988). During the 12 day nursing period, pups use lipid-rich milk from their mother to develop...
a thick blubber layer (Kovacs and Lavigne 1986; Stewart and Lavigne 1980; Worthy 1991; Oftedal et al. 1996). Once weaned, harp seals have 40–50% body fat stored as blubber and begin to molt the lanugo pelt (Worthy 1987; Pearson et al. 2014a). By the time weaned pups begin to swim, the white lanugo coat is completely molted, exposing a black-spotted, silvery pelt (Worthy 1987; Worthy and Lavigne 1987). Over the course of the subsequent 4–5 weeks, harp seals continue to develop, learn how to swim, and transition to independently foraging juveniles (Worthy and Lavigne 1987; Burns et al. 2007; Lestyk et al. 2009).

The primary mechanism through which mammal fur acts as an insulator is by maintaining a stagnant layer of air among the hairs (Hammel 1955; Ling 1970; Kvadsheim and Aarseth 2002). Because stationary air has very low conductivity (Bejan 1990), dry fur prevents heat loss effectively. When phocid fur is submerged, water replaces the air trapped between the hairs of the fur (Liwanag et al. 2012a). Because water has a considerably higher thermal capacity and conductivity than air, submergence reduces the insulation efficiency of the fur dramatically (Scholander et al. 1950; Kvadsheim and Aarseth 2002; Liwanag et al. 2012a; Sharma and Liwanag 2017). Lanugo, or natal fur, of phocid pups is typically denser and longer than adult fur, increasing its insulative capacity (Liwanag et al. 2012a; Gmuca et al. 2015). The guard hairs of adult phocid fur are shorter and flatter to reduce drag while swimming (Liwanag et al. 2012a). Further, fur density decreases with ontogeny, as adult phocids rely on blubber rather than fur for insulation in water and the overall thermal function of adult fur is reduced when submerged (Gmuca et al. 2015; Sharma and Liwanag 2017).

Previous studies have shown for a given thickness and weight, pinniped fur is a more efficient insulator compared to blubber in air (Kvadsheim and Aarseth 2002; Liwanag et al. 2012b; Pearson et al. 2014a). However, because phocid fur is not as thermally effective as blubber once wetted, developing harp seals shift their thermal strategy from reliance on fur to predominantly blubber as they transition to an aquatic lifestyle (Pearson et al. 2014a; Gmuca et al. 2015). Neonates (1 day old) and thin whitecoats (~4 days) have a lanugo coat and very little blubber, whereas fat whitecoats (~9 days) have a lanugo coat and a substantial blubber layer (Pearson et al. 2014a). Ragged jackets (2 weeks old) represent the stage at which pups molt the lanugo coat, and beaters (3 weeks) are fully molted pups. The objectives of this study were: (1) to understand the extent to which the harp seal pelt functions as an insulator in water and (2) to determine the developmental stage at which the overall insulation (pelt and blubber) of a harp seal becomes effective for maintaining thermal homeostasis in water. We hypothesized that the lanugo pelt of pre-molt harp seal pups would exhibit a significant reduction in thermal function in water compared to air, and that this difference would be greater than that observed for the pelt of post-molt animals.

**Materials and methods**

**Sample collection**

Sculps (fur, skin, and blubber) from neonates (within ~24 h of birth, n = 2), ragged jackets (molting pups, 12–15 days old, n = 4), beaters (post-molt pups, ~21 days old, n = 4), and adult female (n = 4) harp seals were collected in March 2008 in the Gulf of St. Lawrence, Canada (47°36′N, 62°13′W). Additionally, sculps from neonatal (n = 4), thin whitecoat (~4 days old, n = 3), and fat whitecoat (~9 days old, n = 4) pups were collected in March 2011 in the “West Ice” off the continent of Greenland (72°24′N, 14°15′W). Together, both sampling periods delineate 5 early developmental stages of harp seals including birth to late weaning, spanning the postnatal molt, with adult samples for comparison. Harp seals were aged following protocols from Stewart and Lavigne (1980). Animals were killed according to approved scientific harvesting methods in Canada and Norway in accordance with Canadian/Norwegian permits for scientific collection. Sculps were collected from the dorsum, just caudal to the shoulders, and samples were imported to the United States with Canadian/Norwegian permits for scientific collection.

**Insulation properties**

The thermal conductivity of pelt samples (cut to approximately 10 × 10 cm) was measured using the standard material method (Kvadsheim et al. 1994; Liwanag et al. 2012a, b). Measurements were performed in a heat flux chamber with a well-insulated lower compartment heated to 37 °C with a circulating water bath (Isotemp®, Fisher Scientific Inc., Pittsburgh, PA, USA), and an ice-chilled upper compartment, as described in Pearson et al. (2014a) and Sharma and Liwanag (2017). To calculate thermal conductivity across the pelt, Fourier’s law was used (Kreith 1958):

\[
H = k \times A \times \Delta T \times L^{-1},
\]

where \(H\) is the heat transfer (J s⁻¹), \(k\) is thermal conductivity (W m⁻¹ °C⁻¹), \(A\) is the surface area (m²) through which the heat is moving, \(\Delta T\) (°C) is the temperature differential across the material, and \(L\) (m) is the material thickness. Assuming heat transfer is equal across the sample and the standard material, the equations for both materials can be set equal and solved for the thermal conductivity of the sample. To account for changes in insulation due to differences in the
thickness of the pelt among age classes, we calculated the thermal resistance \( R \) of the pelt using the following equation:

\[ R = L \times k^{-1}, \]

(2)

A previous study measured the thermal conductivity of the full sculp samples in air (Pearson et al. 2014a), such that pelt and blubber conductivity were determined simultaneously but distinctly and resistance was calculated for each layer.

For measurements in water, the blubber layer was removed from the exact same, previously measured samples, leaving only the skin and fur. Cold water (7.04 ± 4.29 °C; mean ± SD) was poured on top of the sample such that the hairs were completely submerged, and no water flowed beneath the pelt. For neonate and whitecoat samples, the lanugo fur tended to draw water beneath the sample; therefore, we placed a large piece of plastic food wrap under the sample with a cut-out in the center to expose the skin for thermocouple placement. The edges were sealed with silicone (Aquaclear© 100% Silicone Aquarium Sealant, Central Aquatics™, Franklin, WI). This prevented water from wicking beneath the sample. Temperature was recorded every 6 s throughout each 2+ h trial by a Fluke Hydra data logger (model 2625A, Fluke Inc., Everett, WA, USA). The last 30 min of each trial were used for data analysis.

Although pinniped fur typically flattens (i.e., the hairs lie closer to the body) when submerged in water (Sharma and Liwanag 2017), the lanugo fur of neonate and whitecoat (pre-molt) harp seal pups floated away from the skin during water conductivity trials. To quantify the changes in pelt thickness underwater, we compared dry and submerged pelt thicknesses of all age classes. For whitecoat and ragged jacket samples, the pelt was placed in a clear plastic container (15.0 × 15.0 × 6.0 mm). The dry pelt thickness was measured with digital calipers and marked on the container, then water was poured on top of the pelt until it was completely submerged. Changes in pelt thickness were observed horizontally from the right side of the pelt relative to the anterior portion of the sample, as determined by hair orientation. The thickness of the pelt while submerged was marked on the container, and the difference between dry and wet pelt height was measured with digital calipers. Pelt thickness of beaters and adults was measured before and after submersion, since hair did not lift when submerged.

### Heat loss through fur and sensitivity analysis

We calculated average heat loss through the fur layer for each age class in air and conducted a sensitivity analysis on input variables to evaluate effects of changes in properties of the fur on pelt function and thus heat loss. Heat loss through the fur only \( Q_{\text{fur}} \) was calculated from McClure and Porter (1983) as follows:

\[ Q_{\text{fur}} = A[0.94(K_e + K_r)C_1], \]

(3)

where \( A \) is the surface area of the animal (m²; estimated from the ellipsoid model described below), \( K_e \) is the effective heat flow caused by conduction within the fur layer \( (W \ m^{-1} \ °C^{-1}) \), \( K_r \) is the effective heat flow caused by thermal radiation exchange within the fur layer \( (W \ m^{-1} \ °C^{-1}) \), \( C_1 \) is the temperature gradient per unit depth across the fur \( (°C \ m^{-1}) \), and 0.94 is a correction coefficient (McClure and Porter 1983). \( K_e, K_r \), and \( C_1 \) were calculated from equations in McClure and Porter (1983) using data from Gmuca et al. (2015), Pearson et al. (2014a, b), and this study (Table 1). Values used for \( T_s \) and \( T_a \) were empirically measured during the conductivity trials (Gmuca et al. 2015). \( Q_{\text{fur}} \) was compared among age classes using ANOVA.

<table>
<thead>
<tr>
<th>Age class</th>
<th>Hair density ( (\text{hairs} \ m^{-2}) ) ( [\rho_h] )</th>
<th>Hair length ( (m) ) ( [L_h] )</th>
<th>Hair diameter ( (m) ) ( [D_h] )</th>
<th>Ambient temperature ( (°C) ) ( [T_a] )</th>
<th>Skin temperature ( (°C) ) ( [T_s] )</th>
<th>Animal diameter ( (m) ) ( [D] )</th>
<th>Surface area ( (m^2) ) ( [A] )</th>
<th>Fur thickness ( (m) ) ( [Z_f] )</th>
<th>( Q_{\text{fur}} ) (W)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neonate</td>
<td>21,643.883</td>
<td>0.028606</td>
<td>0.0033898</td>
<td>6.23</td>
<td>20.67</td>
<td>0.1554</td>
<td>0.003012</td>
<td>0.023597</td>
<td>2.86 ± 2.17</td>
</tr>
<tr>
<td>Thin whitecoat</td>
<td>20,369.449</td>
<td>0.026648</td>
<td>0.0033125</td>
<td>3.04</td>
<td>17.56</td>
<td>0.2037</td>
<td>0.005061</td>
<td>0.028073</td>
<td>0.69 ± 0.08</td>
</tr>
<tr>
<td>Fat whitecoat</td>
<td>18,737.228</td>
<td>0.027610</td>
<td>0.0030989</td>
<td>2.73</td>
<td>9.13</td>
<td>0.2052</td>
<td>0.005417</td>
<td>0.029795</td>
<td>0.79 ± 0.05</td>
</tr>
<tr>
<td>Ragged jacket</td>
<td>15,401.053</td>
<td>0.024411</td>
<td>0.0033416</td>
<td>4.28</td>
<td>6.29</td>
<td>0.2702</td>
<td>0.010155</td>
<td>0.006777</td>
<td>1.63 ± 0.83</td>
</tr>
<tr>
<td>Beater</td>
<td>13,419.821</td>
<td>0.009491</td>
<td>0.0037187</td>
<td>7.33</td>
<td>8.73</td>
<td>0.2657</td>
<td>0.008458</td>
<td>0.005303</td>
<td>1.14 ± 0.58</td>
</tr>
<tr>
<td>Adult</td>
<td>12,060.645</td>
<td>0.009301</td>
<td>0.0040260</td>
<td>6.66</td>
<td>6.99</td>
<td>0.3881</td>
<td>0.018286</td>
<td>0.006234</td>
<td>0.64 ± 0.55</td>
</tr>
</tbody>
</table>

Parameters listed represent average values for each age class. Data are from Gmuca et al. (2015) and this study. Mean heat loss through the fur \( (Q_{\text{fur}}) \ ± \) SEM is given in the final column. There were no significant differences among age classes \( (P > 0.05) \). The first eight variables were used in the sensitivity analysis and set at two levels, ± 20% of the mean value for each age class.
Sensitivity indices were calculated for eight input variables in the $Q_{fur}$ model (McClure and Porter 1983). We ran a separate sensitivity model for each age class. The eight response variables were set at two levels each ($\pm 20\%$ of the mean of value for each age class). The variables and values used in the sensitivity analyses are given in Table 1. We ran a global sensitivity analysis using the multisensi package in R (Bidot et al. 2018) using a full factorial design, and the results were analyzed with an ANOVA decomposition including the main effects and two factor interactions. Only the main effects are reported.

**Heat loss models**

Mathematical models were used to estimate whole-body conductive heat loss through both the blubber and the pelt (Watts et al. 1993; Kvadsheim et al. 1997). In the primary model, heat loss was calculated using a prolate ellipsoid model, following equations from Mathewson and Porter (2013). Both semi-minor axes were set equal ($a, b$), as height and width measurements were not collected from the animals in the field and the ratio between these two axes is unknown for this species at these age classes (Shero et al. 2014). The major axis ($c$) of the ellipsoid was one half of the standard length (m) of the body from snout to tail. The model simulated an ellipsoid body with a core placed within a uniform layer of sculp (blubber, skin, and fur) (Fig. 1a). Total conductive heat transfer ($\text{Heat}_{\text{Tot}}, \text{W}$) was calculated as heat loss through a layer of insulation surrounding an ellipsoid body. Heat loss was calculated across the sculp, which combines the blubber and fur into a single layer of insulation. We followed Eq. 27 from Mathewson and Porter (2013) as:

$$\text{Heat}_{\text{Tot}} \sim \frac{3k_i V_G b_i b_G}{(\sqrt{3} S_G^3 \cdot (b_i - b_G))} \cdot (T_{MB} - T_A),$$

where $k_i$ is the thermal conductivity (W m$^{-1}$ °C$^{-1}$) of the sculp in air or water, $V_G$ is the volume of the heat generating core model of heat loss, as described by Eq. 5. The model simulates a cylindrical body core placed within a layer of blubber, inside a layer of pelt (skin and fur).

![Fig. 1](image-url) The two geometric representations of seal pup body shape used to model heat loss. **A** Prolate ellipsoid model of heat loss described by Eq. 4. The model simulates an ellipsoid body core surrounded by a layer of sculp (fur + skin + blubber). **B** Cylindrical model of heat loss, as described by Eq. 5. The model simulates a cylindrical body core placed within a layer of blubber, inside a layer of pelt (skin and fur).
tissue (body core; m³), \( b_i \) is the thickness of the core and sculp (m), \( b_G \) is the radius of the body core (m), \( T_{MB} \) is the temperature at the muscle–blubber interface (set to 35 °C), \( T_A \) is the ambient temperature (set to 4 °C for air and −1 °C for water), and \( S_G \) is the shape factor of the body core (m²) as described by Eq. 2 in Porter and Kearney (2009).

The second model represents the traditional method of estimating heat loss in phocids (Kvadsheim et al. 1997) and used a simulated a cylindrical body core placed within a uniform layer of blubber, inside a uniform layer of pelt (skin and fur) (Fig. 1b). The total conductive heat transfer was calculated as:

\[
\text{Heat}_{\text{Tot}} \sim 2 \pi R^2 k_b (T_L - T_H) + \frac{2 \pi L k_p (T_L - T_H)}{z_1 k_o + (z_2 - z_1) k_i} + \left( k_o \ln \left( \frac{R_z}{R} \right) + k_i \ln \left( \frac{R_z}{R_{z_1}} \right) \right),
\]

where \( \text{Heat}_{\text{Tot}} \) is the conductive heat (W) that passes through the blubber and pelt of the ends and trunk of the cylinder, \( R \) is the radius (m) of the body core excluding the blubber and pelt, \( k_b \) is the thermal conductivity (W m⁻¹ °C⁻¹) of the inner insulation (blubber), \( k_p \) is the thermal conductivity (W m⁻¹ °C⁻¹) of the outer insulation (pelt), \( T_L \) is the temperature (°C) of the surrounding air or water (set to −4 °C for water, based on average temperatures during the breeding season; Pearson et al. 2014b), \( T_H \) is the temperature (°C) at the muscle–blubber interface (set to 35 °C), \( z_1 \) is the thickness (m) of the inner insulation (blubber), \( z_2 \) is the thickness (m) of the combined inner and outer insulation (blubber + pelt), and \( L \) is the standard length (m) of the body from snout to tail.

In both models, the radius (semi-minor axis) of the body core was estimated from axillary girth measurements, with girth representing the circumference of a circle including the body core and blubber. Girths and body lengths for neonates and whitecoats were measured upon sample collection (Pearson et al. 2014a). Girths for ragged jackets, beaters, and adult females were estimated from measured mass and standard lengths of individuals, using Eq. 2 from Innes et al. (1981). Body volume was calculated separately for each model as the volume of an ellipsoid or a cylinder. For both models, heat loss was scaled to volume to account for allometric differences in body size and heat loss with age. Thermal conductivity values for the blubber and pelt in air were from Pearson et al. (2014a), and thermal conductivity values for the pelt in water were measured in this study (Table 2).

### Statistical analysis

Pelt conductivity, pelt thickness, pelt resistance, and heat transfer were compared among and within age classes and between treatments (air and water) using a linear mixed model, followed by Fisher’s LSD test. A log transformation was performed on each response variable to achieve homogeneity of variance in model selection. Models included the main effects of age class and treatment, the interaction between the two, and animal ID as a random effect. To compare the results of the elliptical model and the cylindrical model, we used a linear mixed model with log-transformed heat loss by volume as the response, animal ID as a random factor, age class, treatment, and model type (elliptical and cylindrical) as fixed effects. We also included the full factorial interactions between all fixed effects, then used Fisher’s LSD post hoc test. All statistical analyses were conducted using JMP Pro 12 (SAS Institute Inc., Cary, NC).

### Table 2 Model parameters used to estimate heat loss in air and in water

<table>
<thead>
<tr>
<th>Age class</th>
<th>Blubber conductivity (W m⁻¹ °C⁻¹) ([k_b])</th>
<th>Air pelt conductivity (W m⁻¹ °C⁻¹) ([k_p])</th>
<th>Water pelt conductivity (W m⁻¹ °C⁻¹) ([k_p])</th>
<th>Blubber thickness (m) ([z_2])</th>
<th>Air pelt thickness (m) ([z_2-\overline{z_1}])</th>
<th>Water pelt thickness (m) ([z_2-\overline{z_1}])</th>
<th>Body length (m) ([L])</th>
<th>Axillary girth (m) ([R])</th>
<th>Core radius (m) ([R])</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neonate</td>
<td>0.225</td>
<td>0.1317</td>
<td>0.5882</td>
<td>0.0063</td>
<td>0.0236</td>
<td>0.0392</td>
<td>0.868</td>
<td>0.490</td>
<td>0.048</td>
</tr>
<tr>
<td>Thin whitecoat</td>
<td>0.224</td>
<td>0.1523</td>
<td>1.0036</td>
<td>0.0139</td>
<td>0.0281</td>
<td>0.0474</td>
<td>0.873</td>
<td>0.640</td>
<td>0.060</td>
</tr>
<tr>
<td>Fat whitecoat</td>
<td>0.236</td>
<td>0.3696</td>
<td>0.7482</td>
<td>0.0361</td>
<td>0.0289</td>
<td>0.0414</td>
<td>1.023</td>
<td>0.648</td>
<td>0.037</td>
</tr>
<tr>
<td>Ragged jacket</td>
<td>0.209</td>
<td>0.1130</td>
<td>0.3705</td>
<td>0.0458</td>
<td>0.0068</td>
<td>0.0116</td>
<td>0.998</td>
<td>0.913</td>
<td>0.093</td>
</tr>
<tr>
<td>Beater</td>
<td>0.184</td>
<td>0.0832</td>
<td>0.1419</td>
<td>0.0394</td>
<td>0.0053</td>
<td>0.0038</td>
<td>0.878</td>
<td>0.835</td>
<td>0.088</td>
</tr>
<tr>
<td>Adult</td>
<td>0.190</td>
<td>0.0887</td>
<td>0.1151</td>
<td>0.0392</td>
<td>0.0062</td>
<td>0.0041</td>
<td>1.553</td>
<td>1.220</td>
<td>0.149</td>
</tr>
</tbody>
</table>

Parameters listed represent average values for each age class; individual values were used to model heat loss for each seal. Conductivities for blubber and pelt in air were measured in Pearson et al. (2014a); conductivities for pelt in water were measured in the current study. Blubber thickness is from Pearson et al. (2014a); pelt thicknesses are from the current study. Morphometric measurements for pre-molt age classes (neonates, thin whitecoats, fat whitecoats) and body length measurements for all other age classes are from Pearson et al. (2014a). Axillary girth for all other age classes was calculated from Innes et al. (1981).
USA). Where unspecified, $P < 0.05$ was considered statistically significant.

**Results**

**Insulation properties**

There was a significant interaction between age class and treatment for pelt conductivity (W m$^{-1}$ °C$^{-1}$) ($F_{5,19} = 4.97$, $P = 0.0045$; Fig. 2). Pelt conductivity values (Table 2) were significantly higher in water than in air for neonates ($P < 0.0001$), thin whitecoats ($P < 0.0001$), fat whitecoats ($P = 0.031$), and ragged jackets ($P = 0.0006$), but were not statistically different between treatments for beaters ($P = 0.057$) and adults ($P = 0.64$). In air, fat whitecoats had significantly higher pelt conductivity (2–4× higher; 0.3696 W m$^{-1}$ °C$^{-1}$) compared to any other age class (0.0832–0.1523 W m$^{-1}$ °C$^{-1}$; $P \leq 0.0157$), and none of the other age classes were significantly different from each other. In water, pelt conductivity began to decrease at the ragged jacket stage ($P = 0.0358$) then decreased further to and leveled off at the beater and adult stages ($P \leq 0.0078$).

Lanugo pelt hairs were longer than hairs in the juvenile and adult pelts (Table 2; Gmucia et al. 2015). This was reflected in a significantly (approximately 4×) greater pelt thickness for pre-molt (neonate, thin whitecoat, fat whitecoat) pelts compared to molting (ragged jacket) and post-molt (beater, adult) pelts in air ($P < 0.001$; Table 2; Fig. 3). There was a significant interaction between age class and treatment for pelt thickness ($F_{5,19} = 16.01$, $P < 0.0001$). When fully submerged in water, pre-molt pelts had a significant increase in pelt thickness (1.5× thicker; $P \leq 0.0147$) compared to the dry pelt, because the lanugo hairs floated away from the skin. In contrast, beater and adult age classes showed a significant decrease in pelt thickness to ~ 2/3 the pelt thickness in air, associated with hair flattening in water ($P = 0.0099$ and $P = 0.0024$, respectively). Although ragged jackets, which were molting, generally had short hair associated with the new juvenile pelt, the lanugo hairs that remained lifted when submerged (0.0068 m dry to 0.0116 m wet; $P = 0.0003$). In air, pelt thickness was not significantly different for the neonate, thin whitecoat, and fat whitecoat stages, but decreased significantly to ~ 1/4 of lanugo thickness and leveled off at the ragged jacket through adult stages ($P < 0.0001$). In water, neonates, thin whitecoats, and fat whitecoats did not exhibit significant differences in pelt thickness (0.0392–0.0289 m), but pelt thickness decreased significantly (to ~ 1/4 of the thickness of lanugo pelts; 0.0289 m to 0.0068 m) between the fat whitecoat and ragged jacket stages ($P < 0.0001$), then decreased further (to ~ 1/3 the thickness of ragged jacket pelts) between the ragged jacket and beater stages (0.0068–0.0053 m; $P < 0.0002$) where it leveled off into the adult stage (0.0062 m; Table 2; Fig. 3).

Thermal resistance (m$^2$ °C W$^{-1}$) of excised blubber is independent of the treatment because it is a subcutaneous tissue; therefore, the pelt resistance is what drives differences in total insulation in air and in water under laboratory conditions. There was a significant interaction between age class and treatment for thermal resistance of the full sculp ($F_{5,19} = 5.876$, $P = 0.0019$; Fig. 4). Total thermal resistance of the sculp was significantly reduced in water compared with air for neonates ($P < 0.0001$) and thin whitecoats ($P = 0.0001$). In air, total thermal resistance did not change as pups aged, as there were no significant differences among

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![Fig. 2](image2.png)  
**Fig. 2** Mean ± SEM thermal conductivity (W m$^{-1}$ °C$^{-1}$) of harp seal pelts in air (white, data from Pearson et al. 2014a) and in water (black, this study). Different letters represent statistically significant differences among and within age classes and between treatments (air and water) based upon Fisher's LSD test ($P < 0.05$)

![Fig. 3](image3.png)  
**Fig. 3** Mean (± SEM) thickness (mm) of harp seal pelts (skin and fur) in air (white bars) and submerged in water (black bars). Different letters indicate statistically significant differences among and within age classes and between treatments based upon Fisher’s LSD post hoc test ($P < 0.05$). Note that ragged jackets represent the molting stage
age classes. However, in water, neonates and thin whitecoats had significantly lower total thermal resistance compared to all older age classes ($P \leq 0.0096$). After the thin whitecoat stage, total thermal resistance in water increased significantly (by $2\times$) and then stabilized (Fig. 4).

Heat loss through fur

Though there were no significant differences in $Q_{fur}$ among age classes ($F_{5,21} = 0.452, P = 0.807$), in general mean heat loss through the fur was greatest in neonates, followed by ragged jackets, beaters, and adults (Table 1). Fat whitecoats had the lowest mean heat loss through the fur, as they had the thickest pelts (Table 1). The high mean and large variation in $Q_{fur}$ for neonates was driven by one individual animal. When this individual was removed from the analysis as an outlier, neonates had the second lowest mean heat loss through the fur; but there were still no significant differences among age classes ($F_{5,20} = 0.9, P = 0.5$). We examined the input variables and found that pelt thickness for the outlier pup was $\sim 6.5$ times thinner than the average pelt thickness for the other 6 individuals in this study; all other variables were within one standard deviation for the age class. The variation among age classes was driven by the gradient between $T_s$ and $T_a$, and fur thickness and density (Table 1). Generalized sensitivity indices are presented for the main effects in Fig. 5. Within age class, $Q_{fur}$ was most sensitive to changes in fur thickness ($Z_f$) and hair diameter ($D_h$). This was true for all age classes; for adults, these two variables were the only two that showed sensitivity to change in the main effects. Skin temperature was the third most important variable for neonates through beaters.

Heat loss models

Based on our elliptical heat loss model, there was a significant interaction between age class and treatment for heat loss per unit volume ($F_{5,19} = 63.818, P = 0.0146$; Fig. 6). In air, neonates had significantly higher heat loss per unit volume than thin whitecoats ($P < 0.0239$), fat whitecoats ($P = 0.0052$), ragged jackets ($P = 0.0006$), beaters ($P = 0.0039$), and adults ($P < 0.0001$); thin whitecoats had significantly higher heat loss per unit volume than ragged jackets ($P < 0.0001$), beaters ($P = 0.0001$), and adults

![Fig. 4](image-url) Mean thermal resistance ($m^2 \cdot °C \cdot W^{-1}$) of harp seal blubber (gray, data from Pearson et al. 2014a) and pelt in air (white, data from Pearson et al. 2014a) and in water (black, this study). Different letters indicate statistically significant differences for total thermal resistance (pelt and blubber combined) among and within age classes and between treatments based upon Fisher’s LSD post hoc test ($P < 0.05$).

![Fig. 5](image-url) Results of the sensitivity analysis of for eight input variables of the $Q_{fur}$ model (McClure and Porter 1983). Variables are listed in the legend in the same order as shown in each bar. Levels of the variables were set as $\pm 20\%$ of the mean presented in Table 1 for each age class of harp seals. Main effects are shown.

![Fig. 6](image-url) Mean ± SEM heat loss per unit volume (W m$^{-3}$) for harp seals in two treatments (air and water) as calculated from two model types (ellipsoid and cylinder). The three-way interaction between age class, treatment, and model type was not significant, but there was a significant interaction between age class and model type. Thus, different letters indicate statistically significant differences within and between age classes for model type (including both treatments within model type) based upon Fisher’s LSD test ($P < 0.05$).
(\(P < 0.0001\)); and fat whitecoats had significantly higher heat loss per unit volume than all older age classes (\(P < 0.0001\)). In water, neonates and thin whitecoats had the highest heat loss per unit volume (\(P \leq 0.0321\)) compared to all other age classes, fat whitecoats had significantly higher heat loss per unit volume than all older age classes (\(P < 0.0003\)), and ragged jackets had significantly higher heat loss per unit volume than beaters and adults (\(P < 0.0001\)). Between treatments, heat loss per unit volume was significantly higher in water than in air for neonates (\(P < 0.0001\)), thin whitecoats (\(P = 0.0014\)), and ragged jackets (\(P = 0.0089\)); there was no significant difference in heat loss per unit volume between treatments for fat whitecoats, beaters, or adults.

The cylindrical heat loss model produced slightly different results when compared to the elliptical model. Neonates had significantly higher heat loss per unit volume in air than all older age classes (\(P < 0.0039\)), consistent with the elliptical model. However, thin whitecoats had significantly higher heat loss per unit volume when compared to fat whitecoats (\(P = 0.0123\)) and adults (\(P = 0.0190\)), and fat whitecoats did not have significantly different heat loss per unit volume compared to older age classes. In water, neonates and thin whitecoats had the highest heat loss per unit volume (\(P \leq 0.0017\)); however, unlike in the elliptical model, there were no other significant differences among age classes. Between treatments, heat loss per unit volume was significantly higher in water than in air for neonates (\(P < 0.0001\)) and thin whitecoats (\(P = 0.0014\)); there was no significant difference in heat loss per unit volume between treatments for the older age classes, which is inconsistent with the elliptical model.

In the comparison of the elliptical and cylindrical models, there was a significant interaction between age class and model type (\(F_{5,57} = 34.959, P < 0.0001\)), but no significant interaction between treatment and model (\(P = 0.0527\)) or treatment, model, and age class (\(P = 0.1248\)). The cylindrical model significantly underestimated heat loss per unit volume for neonates (\(P = 0.0265\)) and fat whitecoats (\(P < 0.0001\)), and significantly overestimated heat loss per unit volume by \(\sim 2\times\) for ragged jackets (\(P < 0.0001\)), beaters (\(P < 0.0001\)), and adults (\(P < 0.0001\)). There was no significant difference in heat loss per unit volume between the two models for thin whitecoats.

**Discussion**

During early development, harp seals transition from a terrestrial lifestyle to one that is primarily aquatic (Bartholomew 1970; Lavigne and Kovacs 1988). Their insulatory strategy changes as well, as they first rely on their thick lanugo and then switch to blubber as the primary insulator (Worthy 1991; Ofstedal et al. 1996; Kvadsheim and Aarseth 2002; Pearson et al. 2014a). Based on the current study, that shift in insulation is crucial to their successful transition to water because lanugo fur is an ineffective insulator in water. Once the pups have fully molted, there is no longer a significant difference in thermal conductivity of the pelt between air and water (Fig. 2), and it is only after this occurs that pups begin to voluntarily enter the water (Stewart and Lavigne 1980; Kovacs and Lavigne 1985, 1986).

Thermal conductivity measurements give insight into the material properties of an insulation layer, independent of thickness (Kvadsheim et al. 1994). Thermal resistance, which includes both quality (conductivity) and quantity (thickness), gives a more comprehensive and ecologically relevant picture of the efficacy of insulation (Sharma and Liwanag 2017). Based on the thermal resistance values measured in this study, harp seals are thermally capable of entering the water around the fat whitecoat stage (Fig. 4). However, at this stage blood oxygen stores and muscle physiology are not fully developed (Burns et al. 2007; Lestyk et al. 2009) and further physiological development associated with diving may necessitate the postweaning fast.

Previous studies have described the flattening of pinniped hair during submergence, which serves to reduce drag and may also reduce buoyancy during swimming and diving (Fish et al. 2008; Liwanag et al. 2012a). Unlike post-molt hair in harp seals, which flattened, the lanugo of pre-molt and molting pups lifted when submerged (Fig. 3). This phenomenon has not been investigated in other species to date, so it is unknown if this is common among phocid pups. Lanugo guard hairs and underhairs of harp seal pups are approximately \(3\times\) longer, \(1.5\times\) denser, and more circular compared with adult hair (Gmuca et al. 2015). The differences in morphology of the hairs themselves may restrict the ability of hair to flatten when submerged, and the dense nature of the coat may further prevent flattening of the pelt underwater. The lifting of the hairs during submergence may contribute to the reduced thermal function of the pelt in water observed in this study; additionally, it could introduce added drag that may increase swimming costs (Fish et al. 2008). Future research could investigate this phenomenon in other phocid and otariid species.

The sensitivity analysis (Fig. 5) showed that for each age class, fur thickness was the most important variable in determining \(Q_{\text{fur}}\), similar to other species (McClure and Porter 1983). Harp seals appear to reduce \(K_e\), the effective heat flow caused by conduction within the fur, to lower overall heat loss through the fur, as thick fur allows an animal to trap more air next to the skin and reduce \(K_e\). For example, the pelt of the outlier neonate was 6.5 times thinner than the mean for that age class, which resulted in 23 times greater heat loss. We do not know if this individual is a random outlier, or if other neonates are born with similarly thin pelts. However, the magnitude in difference of heat loss through
the fur between a thin pelt and a thick pelt is enough that individuals with thin pelts may be vulnerable even in air, especially at a life stage when there is little blubber insulation to compensate. This may be further compounded in water, where it is likely that when the fur lifts, air is released rather than trapped, and $K_v$ would increase. Changes in hair diameter also affect the amount of air trapped in an area of pelt; the conductivity of hair is approximately 10× greater than the conductivity of air (McClure and Porter 1983). Skin temperature was the third most important variable in all age classes except adults, and in general, post-molt age classes (beaters and adults) had more similar results than pre-molt/molting age classes. In younger animals, the temperature gradient across the fur ($C_1$) was larger because skin temperature ($T_s$) was much higher than ambient temperature ($T_a$), and the trend in $Q_{fur}$ among age classes was driven by this gradient. Values for $T_s$ were measured during the conductivity trials and represent the skin temperature only as a result of heat flow through blubber layer, with no active physiological modifications. As young animals often have poor vasocontrol, these analyses highlight the importance of developing the ability to keep $T_s$ closer to $T_a$ to reduce the temperature gradient as animals begin to molt and fur thickness decreases (Scholander et al. 1950; Irving 1969; Williams et al. 2000). In adults (and beaters to a degree) that rely on blubber for insulation, these two values were already close and $C_1$ was small, so a 20% change in skin temperature or ambient temperature was not important. Heat loss through fur is important, and fur characteristics are likely key to young pup survival; however, as animals age, changes in blubber (thickness, lipid content) are likely more important for insulation.

Seals are not circular and instead fit better into elliptical models due to their fusiform body shape. A previous study showed that using an elliptical model to calculate body composition reduces body volume overestimates, resulting in closer estimates of body mass and composition to empirically measured values (Shero et al. 2014). Indeed, body volume calculated for the cylindrical model was 1.5 times greater than body volume calculated in the ellipsoid model. Kvadsheim et al. (1997) investigated total heat loss in harp seals with a cylindrical model, and did not account for the contribution of fur to insulation, which might explain the authors’ inability to predict empirically measured heat loss rates (Boily et al. 2000). In this study, cylindrical modeling of heat loss overestimated heat loss in both substrates for older age classes (Fig. 6), which is consistent with the overestimation of body volume.

Both models in this study are static models and thus likely underestimate actual heat loss, as air and water moving over the body of the animal would create different boundary conditions affecting convective and radiative heat transfer. Mellish et al. (2015) calculated that radiation contributed $56.6 \pm 7.7\%$ of heat loss in adult Weddell seals, conduction accounted for $27.7 \pm 9.3\%$, and environmental variables such as wind speed and air temperature were also important influences on heat loss. In our conductivity trials, the fur–air interface temperature was ~ 1 °C higher than ambient temperature, and boundary conditions approximated ambient conditions in a controlled environment with no air movement. Empirical measurements necessary to accurately estimate convective and radiative heat loss that would be experienced by animals in a natural environment were not available for the animals in this study. Therefore, our static ellipsoid model of conductive heat loss should be considered a minimum heat loss estimate.

In theory, heat loss per unit volume approximates the amount of energy an animal must expend to maintain euthermy (Scholander et al. 1950). This metric is a good way to determine the relative energetic costs of being in air vs. water at different age classes, at appropriate environmental temperatures. From a thermal standpoint, fat whitecoats could enter the water and not expend additional energy maintaining body temperature. Fat whitecoats represent the age class in which the difference in thermal resistance between air and water declined, and they had the lowest heat loss through the fur layer; it appears fat whitecoats are at a critical stage when both thick lanugo and blubber provide a significant thermal advantage, even if for a short time. This was not the case for other age classes, as the calculated heat loss was significantly higher in the water when compared to air for neonates, thin whitecoats, and ragged jackets. Thus, prior to the beater stage (excluding fat whitecoats), young harp seals may rapidly deplete their limited energy stores if they happen to enter the water for extended periods of time.

Accelerated climate change in the Arctic continues to deplete sea ice coverage and duration (Wood et al. 2015), which is critical for harp seal reproduction and development (Burns et al. 2007; Rosen et al. 2007; Lestyk et al. 2009; Bajszak et al. 2011). Additionally, precipitation as rain in the Arctic is expected to increase (Bintanja and Andry 2017). Given the poor insulative ability of wet lanugo, these increased rain events may further increase heat loss and energy expenditure in young pups. For example, ringed seals have been shown to experience increased mortality due to predation when rain events occur during the period of early development (Taigbøl 1982; Kelly 2001; Stirling and Smith 2004). While long-term changes in Arctic conditions will undoubtedly cause ecosystem-wide spatio-temporal shifts, these episodic events have also been shown to impact survival of phocids (Ferguson et al. 2017). Early age classes are still nursing and have yet to deposit a thick blubber layer, making them especially dependent on a stable sea ice substrate to nurse. If the sea ice retreats before harp seal pups have reached the fat whitecoat stage, pups may be forced to enter the water before they are thermally prepared.
which would increase the risk of mortality at this critical life stage. The accelerated development of harp seals compared with most other phocids appears to be advantageous in their unpredictable pack ice habitat. Overall, the rapid deposition of a thick blubber layer is likely critical for a successful transition from nursing pup to independent juvenile in harp seals.

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