Body and Blubber Relationships in Antarctic Pack Ice Seals: Implications for Blubber Depth Patterns

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ABSTRACT

Morphometrics and blubber depths from all four high Antarctic seals (Weddell, Ross, crabeater, and leopard) were obtained during a midsummer research cruise in the Ross Sea as the physiological ecology component of the U.S. Antarctic Pack Ice Seals project. These data are the only in vivo measurements of all four species from the same location and time of year and focused on variances in morphometrics and blubber depth related to species, sex, and age. By controlling for location and season, this cross-species design provided the means to differentiate how blubber mass might be influenced in these groups. We measured both absolute blubber depth and ratio of blubber depth to body core diameter. We found that adult and younger animals showed differences in blubber depth, but male versus female seals did not show differences within any given species. However, when compared across species, the ratio of blubber ring depth to body core diameter suggests that adult Weddell seals differ in their use of blubber compared with the other three species. We propose that this difference in blubber pattern is most likely related to Weddell nutritional requirements during the breeding season having a greater influence on blubber depth than thermal requirements when compared with the other three species.

Introduction

We report here on one aspect of the ecological physiology component of the U.S. Antarctic Pack Ice Seals (APIS) project. The work was designed to provide a synoptic physiological and morphometric assessment of the four high-Antarctic phocid seal species (Weddell, Leptonychotes weddellii; Ross, Ommatophoca rossii; crabeater, Lobodon carcinophaga; and leopard, Hydrurga leptonyx). The APIS project represents the first examination of all four species handled and sampled in the same region at the same time of year, along with simultaneous oceanographic, genetic, and fisheries data (Ackley et al. 2003).

Blubber serves several functions in phocids, including thermal insulation, streamlining, buoyancy control, and a fuel and metabolic water source. Consequently, the selective pressures for blubber depth are likely to be a combination of these demands, and under variable conditions, any given function may be more dominant. In this experimental capture design, many of those variable conditions were minimized. Because the animals were examined in the same general geographic area and at the same time of year, they were faced with similar thermal, weather, and ice conditions. Further, all seals were captured during the molting, postbreeding season, which simplifies the impact that seasonal physiological differences would have on blubber patterns.

Past studies of in vivo blubber depth in seals have generally followed a paradigm where the morphometrics of individual animals were tracked through time, and changes in the ratio of blubber depth to whole body radius were related to season and thermal insulation (Ryg et al. 1988; Rosen and Renouf 1997). In our study, we offer a somewhat different perspective on the relationship of blubber to the physiology of a phocid.

First, in contrast to previous studies, we used a multispecies approach over a relatively short time frame. While both are powerful methods, the APIS data add a comparative approach wherein different species were measured under the same thermal, spatial, and temporal regimen. This permitted us to test whether different species showed distinct patterns in the relationship of blubber to body core.

Second, the APIS data were derived from much larger phocids than those used in previous studies (Ryg et al. 1988; Rosen and Renouf 1997). Because larger mammals have a lower mass-specific metabolic rate than smaller mammals (Kleiber 1961), we could directly sample animals with different basal metabolic energetics and compare the thermal approach with the relationships of blubber to body core.

Third, no study to date has sampled on such a large scale and conducted in situ experiments in high polar regions. This eliminates potential biases related to sampling in a controlled
environment where the subjects may not necessarily reflect field body condition, field-based diets, field energetic demands, and/or responses to field environmental stressors.

Fourth, in order to examine how blubber depth changed in relation to the metabolically active core, we modified earlier models (Ryg et al. 1988; Rosen and Renouf 1997) that calculated the ratio of blubber depth to whole body radius. In our study, we examined total ring blubber depth in relation to core diameter in order to examine how blubber depth changed in relation to the metabolically active core. Figure 1 compares the previous blubber radius methods with our ring depth/body core method. In this study, we emphasize that the blubber is either a ring of insulation or a fuel source for the core, and therefore, we define our ratio as reflecting the dynamic relationship of the blubber ring depth to the core diameter.

The regulation of blubber is essential in marine mammals, and changes in blubber can be indicative of varied thermal, nutritional, metabolic, and hydrodynamic influences. Consequently, the regulation of blubber depth takes on an ecological perspective as a potential indicator of the physiological health of marine mammals. The studies from the APIS cruise were designed to examine patterns in blubber depth in multiple species under similar in situ conditions to better describe these relationships.

Material and Methods

The APIS cruise traversed the Eastern Ross Sea and into the Western Amundsen Sea in a series of transects up to 500 km offshore (Ackley et al. 2003). All seals were captured within a 6-wk period, from December 27, 1999, to February 13, 2000. Seals were handled using either physical or chemical restraint following approved Marine Mammal Protection Act (MMPA; permit 495-1524) and University of Alaska–Fairbanks (UAF)/Hubbs–SeaWorld Research Institute Institutional Animal Care and Use Committee (IACUC) protocols. Weddell (n = 54), Ross (n = 41), crabeater (n = 65), and leopard (n = 4) seals were measured for morphometrics and/or blubber thickness (Table 2).

Standard length (SL; straight-line distance between tip of nose and tip of tail) was measured along the dorsal side of the animal, and axillary girth was taken just behind the foreflippers, as detailed by Castellini and Kooyman (1990). Mass was measured on a subset (n = 22; as noted in Tables 1, 2) of seals with a hanging electronic load cell (± 0.5 kg; Ohaus I-20W). Blubber depth was assessed using a portable ultrasound device (Scanprobe II, model 7310; Scanco, Wayne, PA) at six sites (hip dorsal and lateral, midbody dorsal and lateral, and axillary dorsal and lateral). This method reflects an ultrasound signal at the interface of blubber and muscle and is routinely used on marine mammals (Gales and Burton 1987; Castellini et al. 1993; Noren et al. 1999; Kvadsheim et al. 2005).

For comparison purposes with the APIS Weddell seals, an additional 14 adult female Weddell seals examined as part of an ongoing project near McMurdo Station during the pupping season were added for the calculation of estimated masses and blubber ratios. For these additional Weddell seals (MMPA 1033-1683; UAF-IACUC 01-06), length, girth, measured mass, estimated mass, and blubber depth were obtained using the same methods and equipment.

Ratios of blubber depth to core diameter were calculated as the mathematical relationship of the core diameter to the surrounding ring of blubber (Fig. 1b). Total body diameter at the axillary site was determined as body girth/π. The total blubber ring depth (2 × blubber depth) was subtracted from the total body diameter to calculate the core diameter. The ratio of the blubber ring to core diameter was then determined as 2 × blubber depth/core diameter at the axillary location. This method is modified from those of Ryg et al. (1988) and Rosen and Renouf (1997), who reported the ratio of blubber depth to the whole body radius (Fig. 1a). While these two values can be converted between one another, our modified method more clearly shows the physiological relationship between the core diameter and the associated blubber layer ring surrounding the core.

Actual mass could not be taken directly from all animals given available on-ice handling time. While mass is not nec-
Morphometrics and Blubber Depth of Antarctic Seals

Table 1: Derived equations and constants for mass prediction based on standard length (L) and axillary girth (G) measurements

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Regression</th>
<th>R²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weddell seals</td>
<td>21</td>
<td>$1.30L \times G^2 \times 10^{-3}/28,300$</td>
<td>.995</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Crabeater seals</td>
<td>14</td>
<td>$1.39L \times G^2 \times 10^{-3}/28,300$</td>
<td>.994</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Ross seals</td>
<td>6</td>
<td>$1.39L \times G^2 \times 10^{-3}/28,300$</td>
<td>.998</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Combined¹</td>
<td>43</td>
<td>$1.31L \times G^2 \times 10^{-3}/28,300$</td>
<td>.994</td>
<td>&lt;.001</td>
</tr>
</tbody>
</table>

Note. Crabeater, Ross, and leopard seals were measured on the APIS cruise. Weddell seal values are from other projects, as noted in the text.

¹ Includes two leopard seals.

For all age groups and both sexes, blubber depth averaged between 20 ± 3 mm for adults and 22 ± 6 mm for pups (Table 2), and blubber/core ratio ranged from 0.075 in larger animals to more than 0.200 in the smallest animal (Fig. 2a). The ratio of blubber ring depth to core diameter for all crabeater seals followed a pattern of increasing ratio with decreasing core diameter ($r^2 = 0.45; P < 0.001$; Fig. 2a).

Results

Crabeater Seals

Seals were assigned an age group in the field (pup, juvenile, adult) on the basis of scarring patterns, size, and behavior. Within any age group, there were no statistical differences between males and females for any of the morphometric indexes, including blubber depths (Table 2). For all age groups and both sexes, blubber depth averaged between 20 ± 3 mm for adults and 22 ± 6 mm for pups (Table 2), and blubber/core ratio ranged from 0.075 in larger animals to more than 0.200 in the smallest animal (Fig. 2a). The ratio of blubber ring depth to core diameter for all crabeater seals followed a pattern of increasing ratio with decreasing core diameter ($r^2 = 0.45; P < 0.001$; Fig. 2a).

Ross Seals

A total of 41 Ross seals were measured during this project. Of these, three were of unknown sex. Using age/length distributions of 40 Ross seals collected during January in the early 1980s by Skinner and Klages (1994), the seals in the APIS study were estimated to be 3–4 yr old. With the crabeater seals, there were no significant differences between male and female Ross seals for any morphometric value. Blubber depth for both males and females averaged 23 ± 3 mm (Table 2). As with the crabeater seals, the Ross seals followed an obvious pattern of increasing blubber/core ratios with decreasing core diameter ($r^2 = 0.56; P < 0.001$; Fig. 2b).

Leopard Seals

Four leopard seals were handled, and they were all males; therefore, no statistical comparisons between sexes were possible. On the basis of age/length data (McLaren 1993), these four males (281 ± 5 cm SL) were estimated to be at least 8–10 yr old. Blubber values were taken on only two animals, and the depth averaged 24 mm, with a smaller blubber/core ratio in the larger animal (Fig. 2c).

Weddell Seals

A total of 41 adult and 13 juvenile Weddell seals were captured on the APIS cruise. Of the adult seals, one male and one female could not be verified for sex. Barring these two animals, there were no sex-based differences in morphometric values within an age class for Weddell seals. Of the four seal species measured, the Weddell seals had the absolute thickest blubber layer and the largest core diameter and were overall the largest seals sampled (Table 2; Fig. 3). The blubber/core ratios for adult Weddell seals did not increase as core diameter decreased (Fig. 2d; $r^2 = 0.005; P = 0.786$). By contrast, in juvenile Weddell seals, the ratio of blubber to core diameter increased as core diameter decreased (Fig. 2d; $r^2 = 0.66; P = 0.050$).

When adult female Weddell seals (APIS) were compared with adult nonparous females measured near McMurdo in November, the McMurdo-based animals were 10% larger in girth ($P = 0.001$), 19% larger in estimated mass ($P < 0.005$), and 55% greater in blubber depth ($P < 0.004$) but no different in SL ($P = 0.256$).

Discussion

Crabeater Seals

Our results are similar to those of Laws et al. (2003), who reported no sex-based differences in crabeater growth curves, body mass, or blubber thickness. Nørdøy et al. (1995) noted that the average mass of eight crabeater seals sampled in late February was 182 kg and determined that the females were heavier than the males. However, SLs were not recorded, and therefore direct comparisons for age and length cannot be made with our results.
Table 2: Values for total number of animals by sex and total handled, length, girth, actual and estimated mass, and average blubber depth (± SD)

<table>
<thead>
<tr>
<th>Species</th>
<th>Animals (n)</th>
<th>Length (cm)</th>
<th>Girth (cm)</th>
<th>Actual Mass (kg)</th>
<th>Estimated Mass (kg)</th>
<th>Blubber Depth (mm)</th>
</tr>
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<tbody>
<tr>
<td>Crab Eaton:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pup:</td>
<td>Male</td>
<td>7</td>
<td>159 ± 7</td>
<td>112 ± 7</td>
<td>107 (1)</td>
<td>94 ± 16</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>2</td>
<td>162 (2)</td>
<td>110 (2)</td>
<td>NS</td>
<td>91 (2)</td>
</tr>
<tr>
<td>Total</td>
<td>9</td>
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<td>112 ± 7</td>
<td>107 (1)</td>
<td>93 ± 16</td>
<td>22 ± 6</td>
</tr>
<tr>
<td>Juvenile:</td>
<td>Male</td>
<td>6</td>
<td>176 ± 6</td>
<td>124 ± 7</td>
<td>146 ± 10 (3)</td>
<td>125 ± 12</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>4</td>
<td>174 ± 8</td>
<td>123 ± 9 (3)</td>
<td>NS</td>
<td>120 ± 19</td>
</tr>
<tr>
<td></td>
<td>Unknown</td>
<td>1</td>
<td>167</td>
<td>117</td>
<td>NS</td>
<td>106</td>
</tr>
<tr>
<td>Total</td>
<td>11</td>
<td>174 ± 7</td>
<td>123 ± 7</td>
<td>146 ± 10 (3)</td>
<td>122 ± 14</td>
<td>21 ± 1</td>
</tr>
<tr>
<td>Adult:</td>
<td>Male</td>
<td>24</td>
<td>208 ± 13</td>
<td>137 ± 9</td>
<td>185 ± 15 (6)</td>
<td>180 ± 25 (21)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>16</td>
<td>206 ± 8</td>
<td>136 ± 5 (15)</td>
<td>198 ± 25 (4)</td>
<td>176 ± 17 (15)</td>
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<td>Unknown</td>
<td>5</td>
<td>203 ± 11</td>
<td>134 ± 5 (5)</td>
<td>NS</td>
<td>169 ± 20 (5)</td>
</tr>
<tr>
<td>Total</td>
<td>45</td>
<td>206 ± 11</td>
<td>136 ± 7</td>
<td>190 ± 19 (10)</td>
<td>177 ± 22 (41)</td>
<td>20 ± 3</td>
</tr>
<tr>
<td>Ross:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult:</td>
<td>Male</td>
<td>25</td>
<td>193 ± 10</td>
<td>134 ± 9 (24)</td>
<td>180 ± 17 (3)</td>
<td>163 ± 26 (24)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>19</td>
<td>191 ± 9</td>
<td>132 ± 7 (13)</td>
<td>118 (1)</td>
<td>153 ± 19 (13)</td>
</tr>
<tr>
<td></td>
<td>Unknown</td>
<td>3</td>
<td>183 ± 15</td>
<td>130 ± 4 (3)</td>
<td>148 (2)</td>
<td>143 ± 16 (3)</td>
</tr>
<tr>
<td>Total</td>
<td>41</td>
<td>191 ± 10</td>
<td>133 ± 8</td>
<td>159 ± 24 (6)</td>
<td>158 ± 24 (40)</td>
<td>23 ± 3</td>
</tr>
<tr>
<td>Weddell:</td>
<td>Adult (APIS):</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>21</td>
<td>217 ± 12</td>
<td>155 ± 11</td>
<td>155 ± 11 (20)</td>
<td>NS</td>
<td>241 ± 38 (20)</td>
</tr>
<tr>
<td>Female</td>
<td>18</td>
<td>219 ± 14</td>
<td>161 ± 11</td>
<td>161 ± 11 (17)</td>
<td>NS</td>
<td>266 ± 50 (17)</td>
</tr>
<tr>
<td>Unknown</td>
<td>2</td>
<td>217 (2)</td>
<td>156 (2)</td>
<td>156 (2)</td>
<td>NS</td>
<td>246 (2)</td>
</tr>
<tr>
<td>Total</td>
<td>41</td>
<td>218 ± 13</td>
<td>158 ± 11</td>
<td>252 ± 46 (39)</td>
<td>NS</td>
<td>30 ± 7</td>
</tr>
<tr>
<td>Juvenile (APIS):</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>7</td>
<td>171 ± 18</td>
<td>131 ± 10</td>
<td>NS</td>
<td>138 ± 30 (7)</td>
<td>26 ± 2</td>
</tr>
<tr>
<td>Female</td>
<td>6</td>
<td>178 ± 19</td>
<td>138 ± 11</td>
<td>NS</td>
<td>159 ± 35 (6)</td>
<td>29 (2)</td>
</tr>
<tr>
<td>Total</td>
<td>13</td>
<td>174 ± 19</td>
<td>134 ± 11</td>
<td>148 ± 34 (13)</td>
<td>27 ± 2</td>
<td></td>
</tr>
<tr>
<td>Adult (McMurdo):</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>14</td>
<td>224 ± 10</td>
<td>177 ± 13</td>
<td>333 ± 55 (13)</td>
<td>316 ± 46 (14)</td>
<td>45 ± 6</td>
</tr>
<tr>
<td>Leopard:</td>
<td>Adult:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>4</td>
<td>281 ± 5</td>
<td>159 ± 6</td>
<td>295 (2)</td>
<td>328 ± 28 (4)</td>
<td>24 (2)</td>
</tr>
</tbody>
</table>

Note. Values in parentheses indicate sample size used for the given parameter. For example, 24 adult male crab eater seals were handled, all 24 were measured for length, 21 were measured for girth, 6 had actual masses collected, 21 had masses estimated, and 12 had blubber measurements taken. Standard deviations are given when n ≥ 3; otherwise, only the average is reported. NS = not sampled. All morphometric combinations within a species were tested for differences as described in the text, but only values in boldface indicate significant differences between two groups. For example, female Weddell APIS and McMurdo seals had significantly different mean values in girth, estimated mass, and blubber thickness.

Our results showed that crab eater seal average blubber thickness was 20–22 mm during the APIS sampling period (December–February). In February–March, Laws et al. (2003) found that the mean blubber thickness of crab eater seals was 33 mm, increasing from approximately 27 mm in first-year animals to 33 mm in third-year animals and up to 38 mm in adults. When both data sets are considered, they suggest a correlation between increasing deposition of blubber and the onset of the fall season.

While the absolute thickness of blubber was not different among crab eater age classes (Table 2), the pattern was such that a relatively greater proportion of blubber was found on smaller seals (Fig. 2a). That is, the smaller animals had a greater ratio of blubber to core diameter than the larger animals. We discuss the thermal and metabolic implications of these findings below.

Ross Seals

Very few Ross seals have ever been handled, and no other expedition has collected as many samples from living animals. Skinner and Klages (1994) report the only other data of a similar sample size (40). However, while they collected in January, their sampling design involved three different years and used lethal methods. Similar to observations from crab eater seals, there were no sex-related differences in gross morphometric values between APIS male and female Ross seals. How-
ever, this finding is not consistent with observations by Skinner and Klages (1994), who reported that mature female Ross seals had greater SL than male seals.

Ours is the first study to record blubber depth data for Ross seals. It also shows the negative relationship between blubber ring depth and body core diameter (Fig. 2).

**Leopard Seals**

There are several reports of leopard seal blubber depth from previous studies, including that of Brown (1957), who noted that the blubber depth of 12 individual seals sampled between April and August varied between 50 and 90 mm. These blubber values are substantially higher than values we recorded in January and early February (Table 2). Walker et al. (1998) reported a value of 45 mm for one 155-kg individual on the sub-Antarctic Island of South Georgia, but there was no time of year reported. On the basis of these minimal observations between APIS and previous studies, it appears that average blubber depth in leopard seals increases during winter months compared with summer months.

With only two leopard seals in this section of the study, it is not possible to draw conclusions about patterns in the ratio of blubber ring depth to core diameter (Fig. 2). However, the larger leopard seal, with a core diameter of 46.6 cm, had much less blubber than Weddell seals of the same core diameter.

**Weddell Seals**

As with the crabeater and Ross seals, there were no sex-based differences in body morphometrics in adult Weddell seals. The most obvious difference between Weddell seals and the other APIS species is in the relationship of blubber ring depth to core diameter. As shown in both Figures 2 and 3, adult Weddell seals did not demonstrate a decreasing ratio as their core diameter increased, while this pattern was seen in juvenile Weddell seals. That is, adult Weddell seals have more blubber for their size than Ross, crabeater, and leopard seals. This finding has a suite of physiological implications, which are discussed in the remainder of this section.

**Implications of Ratios of Blubber Ring Depth to Core Diameter**

Our results show that in crabeater, Ross, and perhaps leopard seals, the ratio of blubber ring depth to core diameter decreases with increasing girth (Fig. 2a–2c). Theoretically, if this pattern...
Figure 3. Ratio of blubber ring depth to core diameter for all four species of seals. Weddell seals from the APIS study are marked by circles, and adult Weddell seals from the McMurdo region are marked by diamonds.

were driven primarily by thermal biology, then smaller animals would have a higher mass-specific metabolic rate, thereby generating more heat, and would need relatively less insulation. However, the increasing surface area to volume ratio with decreasing size and the subsequent relative increase in heat exchange surface area may be a factor that has resulted in the smaller phocids having a relatively greater blubber layer to reduce heat loss. Experiments would need to be designed to measure actual in situ heat flow through the skin of these seals under a variety of thermal conditions to test this concept. For comparative purposes, we calculated the ratios of blubber ring depth to core diameter to be about 0.289 for a ringed seal 24.2 cm in core diameter (Ryg et al. 1988) and about 0.193 for a harbor seal 32.4 cm in core diameter (Rosen and Renouf 1997). These values fall along the same line as those for the Ross, crabeater, and leopard seals, which suggests that the two smaller northern species are selecting for blubber depth similarly.

In distinct contrast, adult Weddell seals did not follow the same pattern in blubber ring depth/core diameter as the other species (Figs. 2d, 3). It appears that this relationship has an inflection point at a 40–42-cm core diameter, with a minimum blubber/core ratio of about 0.100 for seals sampled this time of year. That is, for animals with a core diameter larger than 40–42 cm, the blubber/core relationship begins to stabilize and perhaps reverses as body diameter increases.

Our data suggest that adult Weddell seals have relatively more blubber than the other species sampled in this study. First, this could be a function of mass alone; however, the leopard seals ($n = 2$) sampled in this study were large and did not follow this pattern. Second, it could be related to buoyancy control if Weddell seals require larger relative blubber masses for effective lift because of their particular diving style. It has been shown that freely diving seals will alter their dive profiles and, subsequently, their diving energetics, on the basis of natural seasonal buoyancy differences or when buoyancy is experimentally altered (Webb et al. 1998; Sato et al. 2003; Watanabe et al. 2006).

Third, it could be a function of differences among species in the utilization of blubber during the breeding season. Female Weddell seals nurse their pups in fast ice colonies for about 5 wk (Kaufman et al. 1975; Elsner et al. 1977; Kooyman 1981). During that time, adult females are known to dive (Testa et al. 1989), and some may feed late in the lactation period (Eisert et al. 2005). Very little is known about Ross, crabeater, and leopard seal lactation, but it is thought that their lactation periods are shorter than those of Weddell seals, on the basis of the few observations of mother-pup pairs (Southwell et al. 2003). Southwell et al. (2003) have suggested that the lactation periods of these three pack ice species should be shorter on the basis of the ephemeral nature of pack ice and the fact that earlier studies theorizing longer lactation periods could not be supported.

The overall U-shaped appearance of the relationship between blubber depth and core ratio for Weddell seals contrasts with the linear pattern for this parameter in the other species. For Weddells, the juveniles show the typical declining pattern, and the adults show the flat or increasing pattern. We suggest that this adds further support to the influence of breeding biochemistry on the blubber deposition patterns of adult Weddells that is in some way different from the patterns seen in adult crabeater or Ross seals.

Consistent with that concept, our data show that Weddell seals store relatively larger amounts of blubber than the other Antarctic seals, perhaps because of a greater reliance on energy reserves during the breeding season in the fast ice. However, storage of large amounts of blubber has a metabolic cost associated with it, and recent work on Weddell seals in the McMurdo region suggests that the costs of reproduction (which
would include blubber stores utilized during lactation) negatively impact the survivorship of adult females (Hadley et al. 2007).

In a similarly sized phocid, the northern elephant seal (Mirounga angustirostris), adult females in late molt that had core diameters of 46.9 cm had blubber/core ratios of about 0.140 (D. Crocker, personal communication), which is the average ratio value for APIS adult Weddell seals. Female elephant seals also fast for 4–5 wk during lactation. Combined, these data suggest that the long-duration fasting associated with breeding may be an important factor influencing blubber depth in these two species.

It would be informative to construct comparative blubber depth/core diameter curves for animals in different seasons. We know from this study and previous work that crabeater seals have more blubber by March and that, by November, Weddell seals become much larger (see McMurdo Weddells in Table 2). Unlike the other species, however, we had the opportunity to compare female adult Weddell seals measured on the APIS cruise with other Weddell adult females we measured during the breeding season. Compared with adult nonparous females measured near McMurdo in November, the McMurdo-based animals were 10% larger in girth (P < 0.001), 19% larger in estimated mass (P < 0.005), and 55% greater in blubber depth (P < 0.004) but no different in SL (P = 0.256; Table 2).

These comparative data demonstrate that nonpregnant/nonlactating Weddell seals have significantly more blubber and consequently greater girths and masses during the breeding season in November than during the molt period in January–February. One particular limitation of the APIS study was that we did not know the breeding history of the seals. That is, for the females, some may have nursed and weaned pups, while others may have been nonparous. It has been reported that lactating Weddell seal females lose considerable mass during the breeding season (Tedman and Green 1987; Ireland et al. 2006; Wheatley et al. 2006), but this phenomenon has not been previously recorded for nonlactating animals. Seasonal increases and decreases in phocid mass and blubber depth have been recorded in nonbreeding captive male and female seals, which suggest blubber regulation mechanisms independent of lactation (Rosen and Renouf 1997; Trumble et al. 2006).

The minimum value for the ratio of blubber depth to core diameter would, by definition, alter with changing seasonal depths of blubber. During the season when we would predict that the seals should be the most lean (presumably soon after weaning), the ratio should be at its lowest. Conversely, it should be at its highest during the breeding season, when blubber depths are greatest. For the APIS seals, this means that the minimum blubber depth/core diameter would be specific to the December/February time frame and related to molting condition. If the same experiments were conducted during the time of greatest blubber depth (i.e., during the winter), then the minimum ratio would be higher. Therefore, calculations of energy stores, buoyancy, or thermoregulation that use these blubber depth ratios need to be specific to each species at a particular time of year.

It is apparent that adult Weddell seals do not follow the same pattern of blubber/core ratio during this time of year as the other species sampled during this study. This suggests that Weddell seals are more insulated for their core diameter compared with the other Antarctic seals in the same thermal regime. This would imply fundamentally different thermoregulation control in adult Weddell seals. Recent work has shown that tissue-level aerobic metabolism in Weddell seals is similar to that of terrestrial mammals, on the basis of mitochondrial volume density in locomotor skeletal muscles. This is in contrast to smaller phocids and subadult Weddell seals, which are shown to have elevated aerobic capacities (Kanatous et al. 2008). While similar studies have not been conducted on the other three APIS species, if Weddell seals have a lower overall metabolic rate, then they may need greater amounts of blubber insulation to maintain thermal balance.

As we noted earlier, the amount of blubber on a seal is a result of a combination of thermal, buoyancy, energetic, and water balance demands. All of these most likely play roles in why the blubber pattern is different in Weddell seals than in the other Antarctic phocids, although the energetics of breeding may be dominant in this case. Each role would need to be explored in more detail to design experimental protocols that might be able to separate them.

Conclusions

On the basis of the data presented here, we make the following conclusions. (1) No sex-based morphometric differences exist within any given age class of crabeater, Ross, or Weddell seals during the January–February summer season. (2) Blubber thickness for Weddell, crabeater, and leopard seals appears to be thinner at this time of year (austral summer) than at other seasons. Ross seal blubber depths have not been previously reported, but in this study, they were similar to crabeater blubber depths. Weddell blubber depths were the greatest in all four species. (3) The ratio of the blubber ring depth to the core diameter increased with decreasing core diameter for all seals except adult Weddell seals. Adult Weddells appeared to stabilize or reverse that trend in what may be an adaptation for increased blubber stores utilized for fasting periods associated with breeding.

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**Literature Cited**


