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Body condition as an index of winter foraging success in crabeater seals (*Lobodon carcinophaga*)

Birgitte I. McDonald[a,*], Daniel E. Crocker[b], Jennifer M. Burns[c], Daniel P. Costa[a]

[a]*Long Marine Laboratory, Department of Ecology and Evolutionary Biology, University of California Santa Cruz, 100 Shaffer Road, Santa Cruz, CA 95060, USA*
[b]*Department of Biology, Sonoma State University, 1801 East Cotati Avenue, Rohnert Park, CA 94928, USA*
[c]*Department of Biological Science, University of Alaska, 3211 Providence Dr., Anchorage, AK 99508, USA*

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Abstract

Body composition is a direct measure of body condition and as such integrates seasonal variation in foraging success and energy expenditure. In phocids, body condition is a critical determinant of both reproductive effort and ability to survive periods of poor foraging success. We determined body composition in 29 crabeater seals, *Lobodon carcinophaga*, during austral autumn (April–May 2002) and late winter (August–September 2001, 2002) off the Antarctic Peninsula by measuring blubber depth and taking morphometric (length, girth) measurements. In 15 of these seals, we also measured body composition using the labeled-water dilution technique. The two methods produced similar body composition estimates, with an average difference of 7%. There were no differences in body composition between adult males and females or between autumn and late winter. These findings suggest that by autumn, adult seals have replenished their energy stores following reproduction and molt. Similarly, the absence of seasonal variation in adults indicates that seals are successfully foraging throughout winter. In addition to providing insight into seasonal and age-related variation in body composition, this study provides baseline body condition data that can be used to measure impacts of natural or anthropogenic environmental change on one of the large consumers of Antarctic krill.

Keywords: Marine mammals; Body conditions; Body composition; Seasonal variations; Foraging behavior; Crabeater seals

1. Introduction

One of the main goals of the US Southern Ocean GLOBEC (GLOBal ocean ECosystems dynamics) research program has been to link shifts in predator and prey dynamics with environmental variability (Hofmann et al., 2002). Recent research has focused on using apex predators as indicators of marine resources (Boyd and Murray, 2001; Reid et al., 2005), as changes in food availability can affect reproductive success and population growth in many of these species (Trillmich et al., 1991; Reid and Forcada, 2005). In phocids, body condition, defined as degree of fatness for this study, has been shown to be an important determinant of reproductive success because adults rely on stored energy reserves to sustain them during the breeding season (Costa, 1991; Crocker et al., 2001b). Similarly, animals with larger energetic reserves are better able to withstand periods of reduced foraging, such as may occur during molt, or when food availability is low (Hindell et al., 2003).

Because body condition integrates day-to-day variation in foraging success and is correlated with future survival and reproduction (Caughley, 1977; Lockyer, 1986; Harwood et al., 2000), measures of body condition provide a valuable tool for evaluating both the health of populations and individuals (Derocher et al., 2004). Marine mammals store energy primarily as lipid in a hypodermal blubber layer that is also important in thermal regulation and buoyancy (Ryg et al., 1988; Webb et al., 1998). The amount of blubber has been considered the best indicator of body condition (Lockyer, 1986; Read, 1990); however,

*Corresponding author. Tel.: +1 831 459 2691; fax: +1 831 459 3383.
E-mail address: mcdonald@biology.ucsc.edu (B.I. McDonald).

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estimating blubber content of animals has proven to be difficult using non-invasive techniques.

Body composition can be measured using the labeled-water technique (Bowen and Iverson, 1998; Speakman et al., 2001). In this technique, estimates of total body water are combined with estimates of tissue hydration state to derive total lipid mass. While generalized equations relating TBW to lipid mass exist, ideally this correlation should be determined empirically for each species under study (Reilly and Fedak, 1990). This method works well in fasting animals (Reilly and Fedak, 1990; Gales et al., 1994), but can result in underestimates of lipid mass in feeding animals due to the water content of the gut (Speakman et al., 2001). Alternatively, body composition can be estimated by measuring the animal's length, girth, and blubber thickness at various sites on the body (Slip et al., 1992; Gales and Renouf, 1994; Webb et al., 1998). This technique has been shown to be an accurate estimate of lipid content in southern and northern elephant seals (Slip et al., 1992; Webb et al., 1998) and harp seals (Gales and Renouf, 1994). Since this method is based on estimating the volume of the subdermal blubber layer it seems to work well with phocids, whose fat reserves are largely subcutaneous (Bryden, 1967; Gales and Renouf, 1994). However, it may be less accurate in species that store significant lipid inside the body cavity or within muscle.

Crabeater seals, *Lobodon carcinophaga*, are an important predator in the Southern Ocean. They have a circumpolar distribution and are the most abundant pinniped with population estimates ranging between 12 and 15 million (Erickson and Hanson, 1990; Costa et al., 2006). During summer, crabeater seals feed primarily on Antarctic krill (*Euphausia superba*) in the upper 50 m of the water column (Nørdoy et al., 1995), and may consume more krill in the Southern Ocean than whales (Hewitt and Lipsky, 2002). While crabeater seal foraging behavior has been studied during the summer months (Øritsland, 1977; Nørdoy et al., 1995), little is known about crabeater seal or krill behavior in winter (Hofmann et al., 2002; but see Burns et al., 2004).

During the autumn and winter, Southern Ocean GLOBEC cruises of 2001 and 2002 Antarctic krill and other large zooplankton were virtually absent from the surface waters (Ashjian et al., 2004; Lawson et al., 2004; Zhou and Dorland, 2004) and there was a decrease in zooplankton biomass from autumn to winter (Lawson et al., 2004). During this period, crabeater seals dove much deeper and longer than recorded during summer months, and also included fish in their diet (Burns et al., 2004). These changes in behavior may reflect shifts in prey density and availability in the surface waters (Burns et al., 2004). Although satellite tracking and diving data present clear evidence that crabeater seals are modifying their foraging behavior to deal with changes in krill distribution and abundance, it is not clear how these changes impact foraging success during winter.

In order to determine if winter is a time of food stress for crabeater seals we assessed body condition during the austral autumn and winter using two different techniques. The specific aims of this study were to (1) examine seasonal variation in body condition to determine foraging success over the winter; (2) establish a baseline body condition for crabeater seals in autumn and winter to help monitor the health of the population as environmental conditions change; and (3) compare the morphometric and labeled dilution methods for estimating body composition.

2. Methods

As part of the Southern Ocean GLOBEC winter cruises, 35 crabeater seals (14 adult females, 17 adult males, 2 juvenile females, and 2 juvenile males) were captured in the Marguerite Bay Region (~67°S, 67°W) during three research cruises (21 July–1 September 2001 ($n = 7$), 7 April–21 May ($n = 14$), and 29 July–19 September 2002 ($n = 14$)). Seals were sighted from the bridge of the R.V. Lawrence M. Gould and approached by foot or via a small boat depending on ice conditions. Seals were initially sedated by an intramuscular injection of Midazolam (0.39–0.84 mg kg^{-1}; Hoffmann-La Roche Inc., NJ, USA) using a pole syringe. After waiting 20 min seals were manually restrained with a hoop net and isoflourine was delivered using a circle rebreathing circuit via gas mask or intubation (Gales et al., 2005).

Seals were weighed in a sling using a hand winch and scale (Ohaus I-20W capacity 1100 ± 0.5 kg) suspended from a tripod. Body composition was determined using a combination of ultrasound and morphometric measurements. Blubber depth measurements were taken using an ultrasound scanner (Scanoprobe II, Ithaca, NY, USA) at 15 uniform sites along the seals' body in combination with seven measurements of both length and girth along the seals' body (Fig. 1). These measurements were used to model the seal as a series of truncated cones. Volumes of blubber and non-blubber compartments of each cone were calculated and summed to estimate total body composition (Gales and Burton, 1987; Webb et al., 1998; Field et al., 2002). Assuming densities for the two compartments of 0.94 and 1.1 g ml^{-1}, respectively (Gales and Burton, 1987), the relative proportion of mass attributable to each was calculated. As a verification of body composition determination, body mass determined by weighing was compared to the body mass calculated by from the morphometric measurements. Body composition data was excluded for seals whose calculated mass was 5% greater or less than the actual mass, resulting in 29 useable body composition measurements. The average calculated mass error in these 29 measurements was 0.9%.

Body composition on 15 of these seals also was determined using the labeled-water dilution method. Initial blood samples were collected from the extradural vein in serum vacutainers (no anticoagulant) for determination of background isotope levels. Seals were given an injection of 1.5 mCi of tritiated water (HTO) and serial blood samples were collected in serum vacutainers at 15–30 min intervals

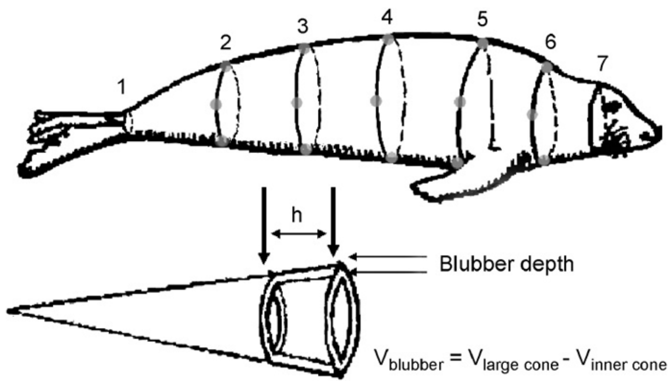

Fig. 1. Morphometric measurements on a crabeater seal. Girth measurements were made at each of the seven rings. Ring 1 is located at the base of the tail. Ring 5 is the axial girth located at the base of the foreflippers. Ring 7 is located at the ears of the seal. Rings 2–4 area evenly spaced between rings 1 and 5. Ring 6 is halfway between rings 5 and 7. Length measurements were taken along the back of the seal from the nose to each ring and the tip of the tail. Three blubber depth measurements were taken at the girth locations 2–6 (dorsal, lateral, and ventral: gray dots). Body composition was determined from length, girth and blubber depth measurements by treating the seal as a series of truncated cones (based on Gales and Burton, 1987).

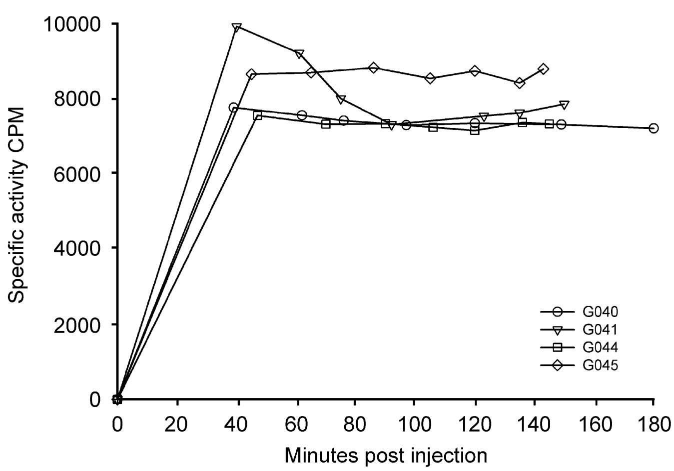

Fig. 2. Specific activity of tritium in blood samples of four adult crabeater seals plotted against time after injection of isotope. Equilibration time of tritium with total body water was complete within 90 min post-injection.

up to 1.5–3 h post-injection to determine equilibration time. Equilibration occurred within 90 min (Fig. 2), so samples collected after 90 min were averaged and used as the equilibrium value. Blood samples were centrifuged and serum was collected for total body water determination.

Immediately before analysis, serum samples were thawed and water extracted by heat distillation (Ortiz et al., 1978). The specific activity of tritium in 100 μl of the distillate was determined in triplicate in 10 ml of scintillation cocktail with a liquid scintillation counter (Beckman LS 3801) along with a dilute HTO standard to calculate the activity of tracer injected. Total body water (TBW; kg) was determined as the activity of injected isotope divided by the activity in the post-equilibrium samples. Values were reduced by 4% to correct for the overestimation of the labeled-water dilution method (Nagy and Costa, 1980; Bowen and Iverson, 1998; Speakman et al., 2001). Fat mass was determined from TBW using the equation (Iverson et al., 1993; Webb et al., 1998):

$$M_{\mathrm{F}} = M_{\mathrm{T}} - 1.37 \times \mathrm{TBW}$$

where M_{F} is the fat mass (kg) and M_{T} is the total body mass of the seal (kg).

In order to compare the body composition measurements from the ultrasound/morphometric and labeled-water dilution techniques, the fat mass determined from the labeled-water technique was converted to percentage blubber mass by assuming blubber contains 90% lipid (Crocker et al., 2001a).

All data passed tests for normality and homogeneity of variances. Body composition determined from the morphometric and labeled-water methods were compared. Sex and seasonal differences in mass, length, body composition, and dorsal sternum blubber depth (determined from ultrasound) were examined. Multiple ANOVA's were conducted; however, the interaction term was never significant, so season and sex were examined independently. Although blubber depth is not the best indicator of body composition (Ryg et al., 1990), we included it here for comparisons with previous studies conducted in the same region in the 1960s and 1970s (Øritsland, 1970; Laws et al., 2003). Comparisons also were made between adult and juvenile animals, but no statistics were performed due to the limited sample size of juveniles ($n = 2$). Annual variability was examined using a t-test comparing winter 2001 and winter 2002 data. Data are presented as mean ± standard deviation. Values were considered significant if $P<0.05$. All statistics were performed in Systat 10.2.

3. Results and discussion

3.1. Comparison of morphometric and water dilution techniques

Due to the complications of using the labeled-water dilution technique in a feeding seal, we feel that the morphometric measurements are a more reliable measure of body composition. On average, the mean body composition measured by the two methods differed by 2.1% (morphometric method = 37.6 ± 3.4% blubber, labeled-water dilution = 35.7 ± 6.1% blubber). At the individual level, the percent body fat estimated by the ultrasound/morphometric method overestimated that determined by the labeled-water dilution method (mean error = 7.9 ± 15.8%, range = −9.3% to 45.2%). However, the results from the two methods were significantly correlated (Fig. 3; Pearson correlation coefficient = 0.72, $P = 0.003$) and not significantly different (paired t-test, $t_{14} = 1.74$, $P = 0.10$).

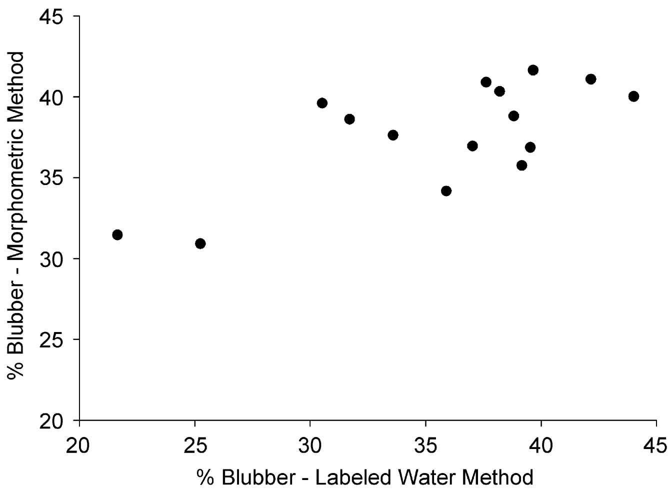

Fig. 3. Comparison of percentage blubber obtained using the labeled-water and morphometric methods. The percentage blubber obtained using the two methods were correlated (Pearson correlation coefficient = 0.72, $P = 0.003$).

The labeled-water dilution technique has been found to accurately measure body composition in many field situations (Slip et al., 1992; Gales et al., 1994), and (in the absence of direct measures) is typically used as the standard against which other methods are assessed. However, in this study crabeater seals were handled soon after hauling out on ice floes, and may recently have been feeding (Burns et al., 2004). In this case, measures of TBW would likely include the water in the gut, and so under-estimate total body fat (Speakman, 1997). If this is the case, the greater variability in TBW estimates as compared to the morphometric technique, might be related to the time since ingestion and meal size.

In contrast, the morphometric technique does not suffer from this potential source of error. However, it is based on the assumption that most of the seals' fat is in the blubber layer. This assumption has been validated in several phocid species (Bryden, 1967; Gales and Renouf, 1994; Kanatous et al., 1999, 2002). Complications also can arise if muscle is mixed in with the blubber layer (as in otariids) because the ultrasound would interpret these layers as the blubber/muscle boundary. This is not seen in most phocids. Another important factor that could potentially explain the discrepancies in comparing the two methods is the hydration state of blubber. To convert the fat mass calculated using the labeled-water dilution technique to percentage blubber we assumed that the water content of blubber was 10%. However, research in other species has found that the hydration state of blubber can vary with age, season, and condition by as much as 16% (Beck et al., 1993; Gales et al., 1994; Crocker, 1995).

The ultrasound/morphometric method has been shown to be appropriate at addressing condition in southern and northern elephant seals (*Mirounga leonina*, *Mirounga angustirostris*) and harp seals (*Phoca groenlandica*) (Slip et al., 1992; Gales and Renouf, 1994; Webb et al., 1998). Results from this study suggest that the morphometric method is also appropriate for estimating body composition in crabeater seals. It is also a simple, non-invasive procedure that can be used easily to monitor the condition of crabeater seals. In other phocids species, both methods have proven to be powerful tools is assessing body condition (Slip et al., 1992; Gales and Renouf, 1994; Gales et al., 1994). In order to determine how accurately they assess body composition both methods would need to be tested empirically and equations calculated specifically for crabeater seals (Reilly and Fedak, 1990; Gales et al., 1994). However, that was beyond the scope of this study. For the remainder of the analyses only percentage blubber determined using the ultrasound/morphometric method was used because the two methods were comparable and that allowed for a larger sample size.

3.2. Gender and seasonal differences in body composition

Adult females were slightly but significantly heavier (Table 1: $F = 4.736$, $P = 0.040$) and longer ($F = 4.453$, $P = 0.046$) than adult males. In a larger sample size ($n = 1146$) collected between 1967 and 1978, Laws et al. (2003) also found that females tended to be larger than males of a similar age. Unfortunately, we do not have any information on age in our sample. However, most pack ice species are monomorphic or exhibit slight reverse sexual dimorphism (Reidman, 1990). Although female crabeater seals tended to be larger, there was no difference in body composition (Table 1: $F = 2.258$, $P = 0.147$) or blubber depth ($F = 0.777$, $P = 0.387$). This is consistent with previous research in crabeater seals (Øritsland, 1970; Laws et al., 2003), leopard seals (*Hydrurga leptoyx*) (Øritsland, 1970), and harp seals (Gales et al., 1994). While most studies examined sex differences during one season of the year, male and female size and condition may differ depending on the season (Beck et al., 1993, 2003; Andersen et al., 1999). For example, in harp seals, females have less blubber than males only in winter (Beck et al., 1993). In contrast, we found no difference between male and females during autumn or winter and no interaction between season and sex ($P > 0.05$).

There were no seasonal differences in mass (Table 1: $F = 0.417$, $P = 0.525$), length ($F = 3.054$, $P = 0.094$), body composition ($F = 0.000$, $P = 0.995$), or sternum blubber depth ($F = 2.439$, $P = 0.132$) for all animals, indicating that during winter crabeater seals find sufficient prey to maintain their body condition. We compared our results to blubber depth data collected in the 1960s and 1970s to put these data in a larger seasonal context (Fig. 4). This comparison suggests that crabeater seals quickly increase energy stores in late summer/early autumn between February and March and maintain these levels throughout winter (Laws et al., 2003), perhaps even increasing in early spring, prior to the onset of breeding (Øritsland, 1970). During the breeding season, blubber thickness declines, as would be expected for a capital breeder (Øritsland, 1970).

Table 1
Age, gender, seasonal and annual comparison of mass, length, percentage blubber (as determined from morphometric method) and sternum blubber depth (mean ± S.D.)

	n	Mass (kg)	Length (cm)	Body composition (% blubber)	Sternum blubber depth (cm)
Sex[a]	12	**267 ± 34**	**228 ± 10**	37.8 ± 2.0	4.3 ± 0.5
Adult female	15	**243 ± 27**	**221 ± 9**	38.8 ± 2.0	4.3 ± 0.3
Adult male					
Season					
Autumn	10	250 ± 36	221 ± 9	38.4 ± 2.3	4.2 ± 0.4
Winter	17	256 ± 30	226 ± 10	38.4 ± 1.9	4.3 ± 0.4
Year[b]					
Winter 2001	6	270 ± 30	230 ± 11	39.2 ± 1.7	**4.6 ± 0.2**
Winter 2002	11	248 ± 28	224 ± 9	38.4 ± 1.9	**4.2 ± 0.4**
Age class[c]					
Juveniles	2	137 ± 28	185 ± 11	31.2 ± 0.4	2.5 ± 0.3
Adults	27	253 ± 32	224 ± 10	38.4 ± 2.0	4.3 ± 0.4

Values in bold are significantly different.
[a]Adult females were significantly heavier and longer than adult males.
[b]Sternum blubber depth was greater in 2001.
[c]No statistics were done due to small juvenile sample size.

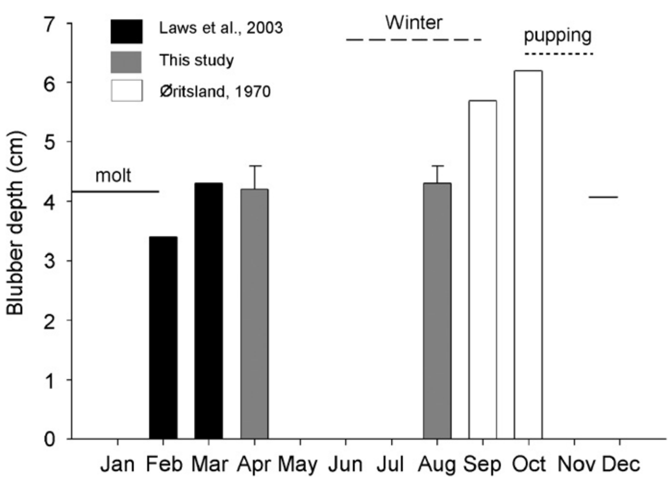

Fig. 4. Seasonal variation in mean sternum dorsal blubber depth. February–March data were collected between 1969 and 1972 in Marguerite Bay (only adult values included; Laws et al., 2003). September–October data were collected in 1964 in the South Shetlands Island region (Øritsland, 1970). The seals have a thick blubber layer in October at the start of breeding which decreases substantially over the summer, when the seals breed and molt. After the seals molt, there is a rapid increase in fat which they maintain throughout the winter.

That the values measured in this study during both autumn (April/May) and winter (August/early September) are similar to those measured by Laws et al. (2003) in March suggests that crabeater seals have an annual cycle of fattening before the energetically demanding reproductive and molt seasons (Andersen et al., 1999; Beck et al., 2003), when ocean productivity is increasing and krill are closer to the surface (Veit et al., 1993; Lascara et al., 1999).

Changes in body condition between studies can also reflect annual differences in food availability. For example, in this study, there was a tendency for seals captured in winter 2001 to be heavier and have more blubber (as a percent body mass and blubber depth) than seals captured in winter 2002 (Table 1: mass $t_{15} = 1.47$, $P = 0.173$, % blubber $t_{15} = 1.40$, $P = 0.189$, blubber depth $t_{15} = 2.53$, $P = 0.024$). Due to lack of body condition data in autumn of 2001 no comparison was made between years for the autumn. Similarly, Laws et al. (2003) found that crabeater seals captured in 1969 had a sternum blubber depth that was 42% greater than animals captured in 1971 (4.7 cm vs. 3.3 cm). These findings suggest that in addition to monitoring the health of the crabeater seal population, we may also be able to use body condition to get a better understanding of the status of their primary prey species.

In addition to maintaining positive energy balance, crabeater seals in this study were in good condition. Body composition and blubber depth measurements obtained during autumn and winter fall in the upper range in what has been measured in other polar phocids (Table 2). Additionally they are in similar condition to crabeater seals studied in Marguerite Bay in the 1960s and 1970s. Seals in our study were on average heavier (245.5 kg) that seals in the 1970s (~200–220 kg; Laws et al., 2003). The earlier study was conducted in February and early March so the difference is likely due to the fattening period indicated by the blubber depth data.

Two of the 29 seals were classified as juveniles (<2 years) based on their length and mass (Laws et al., 2003). Juveniles had lower body condition and sternum blubber depths than did adults (Table 1). Laws et al. (2003) also found that juveniles had smaller sternum blubber depths than adults, approximately 2.7 cm vs. 3.7 cm in adults. This is similar to findings in harbor seals (*Phoca vitulina*) where juveniles have both a lower body condition than adults (Burns et al., 2005) and do not exhibit the seasonal variation in blubber depth exhibited by adults (Pitcher, 1986). Juveniles might have lower lipid reserves due to a greater investment towards growth than storage or lower foraging success due to physiological constraints or lack of experience. Reduced oxygen stores and

Table 2
Summary data on body composition and blubber depth for selected polar phocids

Species	% Blubber[a] (range)	% Lipid[b] (mean or range)	Blubber depth (mean or range) (cm)	Time of year	Source
Southern Hemisphere					
Crabeater seal—*Lobodon carcinophaga*	30.9–42.5		4.2	April/May and August/September	This study
			5.7	September/October	Øritsland (1970)
			3.3	February/March	Laws et al. (2003)
		20.4		January/February	Bryden and Erickson (1976)
Leopard seals—*Hydrurga leptonyx*			4.6	September/October	Øritsland (1970)
Ross seal—*Ommatophoca rossii*			5.6	September/October	Øritsland (1970)
	23–24			January/February	Bryden and Erickson (1976)
Weddell seal—*Leptonychotes weddellii*		19.0–45.7		October–December	Wheatley et al. (2006)
Northern Hemisphere					
Bearded seal—*Erignathus babatus*	25–38			May	Ryg et al. (1990)
			3.7–6.0	May–September	Andersen et al. (1999)
Ringed seal—*Phoca hispida*	15–50			February–September	Ryg et al. (1990)
Hooded seal—*Cystophora cristata*		24.7–28.1		March	Mellish et al. (1999)
Harp seal—*Phoca groenlandica*	15–39			January/February	Ryg et al. (1990)
	18.5–37.8				Gales and Renouf (1994)
			3.3	March/April	Nilssen et al. (1997)
			2.2	June	Nilssen et al. (1997)
			8.8	October	Nilssen et al. (1997)

[a]Percentage blubber includes the water and lipid in the blubber layer.
[b]Percentage lipid is the total lipid in the seals (including non-blubber layer fat).

higher mass specific metabolic rates (Gentry et al., 1986; Costa, 1993; Burns et al., 2005) may be especially challenging for juveniles during winter when krill is found at a greater depth (Ashjian et al., 2004; Lawson et al., 2004; Zhou and Dorland, 2004). However, although juveniles have lower lipid reserves, this does not necessarily mean that they are in poorer condition than adults. Juvenile seals may have lower requirements for storage due to the absence of reproduction.

In summary, these findings suggest that crabeater seals are able to maintain or increase body mass and condition while foraging in winter despite reduced light levels, and shifts in the depth distribution and abundance of their primary prey species, Antarctic krill. In addition, the morphometric method proved to be a useful technique in accessing condition in crabeater seals and will be a valuable tool to access how crabeater seals and their prey are responding to changes in the environment.

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