

Ecological Implications of Body Composition and Thermal Capabilities in Young Antarctic Fur Seals (*Arctocephalus gazella*)

Matthew R. Rutishauser^{1,*}

Daniel P. Costa¹

Michael E. Goebel²

Terrie M. Williams¹

¹Long Marine Laboratory, 100 Shaffer Road, Santa Cruz, California 95060; ²National Oceanic and Atmospheric Administration/National Marine Fisheries Service, Antarctic Ecosystem Research Division, P.O. Box 271, La Jolla, California 92038

Accepted 12/17/03

ABSTRACT

In comparison with other homeotherms, young recently weaned marine mammals in high latitudes face exceptional energetic demands when foraging and thermoregulating. Lipids are an important source of energy and a major component of insulation that allows them to meet these demands. To examine the role of lipid stores in a high-latitude pinniped, we measured the body composition and thermoregulatory capabilities of Antarctic fur seal (*Arctocephalus gazella*) pups and yearlings by using flow-through respirometry and hydrogen isotope dilution. From these data, we constructed a model to examine the importance of postweaning fasting capability in free-ranging young fur seals. Resting metabolic rates were different for pups and yearlings measured in 0.6°C water, 10.3°C water, and ambient air; however, mass and percent lipid as covariates accounted for the different metabolic responses in pups and yearlings for all treatments. The estimated lower critical temperature for combined pups and yearlings was 14.4°C, 10°–15°C above water temperatures normally experienced by Antarctic fur seals. Modeling predicted that a weaned fur seal pup would survive at sea from 9.8 to 36.2 d before succumbing to starvation. The most likely maximum travel distance within this time constraint suggests that food resources close to the natal rookery are important to first-year survival for this species.

Introduction

First-year survival is a critical part of life history in long-lived vertebrates (Begon and Mortimer 1986), often impacting the population dynamics of a species (York 1994; Craig and Ragen 1999). Life-history strategies, energy stores, the physical environment, and resource requirements are some of the factors that dictate success. In general, young animals are more challenged than adult animals and experience lower annual survival (Begon and Mortimer 1986; Hindell 1991). For example, juveniles may be physiologically unprepared for the rigors of their early life as well as naïve with regard to appropriate foraging strategies and behaviors. Young homeotherms also have a higher surface-area-to-volume ratio than adults, potentially increasing the energetic cost of thermoregulation due to high heat loss (Irving and Hart 1957).

Perhaps the most challenged of newly independent animals are high-latitude marine mammals. They are often weaned far from food resources and live in a highly challenging thermal environment. Moreover, diving is a critical aspect of foraging in marine mammals and requires that the animals meet the physiological challenges of submergence in order to forage successfully. Because of their small size and immature physiology, young animals have reduced diving capabilities relative to adults (Kooyman et al. 1983; Burns and Castellini 1996; Burns 1999), making adult prey resources difficult or impossible to use (Hindell et al. 1999).

Increasing insulation by adding a blubber layer, composed primarily of lipid, is one way a young animal can overcome the challenge of thermoregulation (Young 1976). Lipid is typically acquired during the period of maternal investment as assessed by milk intake, mass gain, or total body lipid stores (Ortiz et al. 1984; Costa and Gentry 1986; Costa 1987; Higgins et al. 1988; Hood and Ono 1997; Lea and Hindell 1997). Milk is received in excess of the immediate energetic demands of the animal, allowing for growth, buildup of a blubber layer, and storage of lipid for future energy needs. As a result, maternal investment through the delivery of lipid likely mitigates the difficulties associated with transitions to independence, thereby increasing survivorship of newly independent offspring (Blueweiss et al. 1978; Baker and Fowler 1992; McMahon et al. 2000).

However, the role of lipids in young marine mammals is more complex because it serves a dual role as insulator and energy store (Bryden 1968; Stewart and Lavigne 1980; Ryg et al. 1988). Animals can thermoregulate in several ways: (i) el-

* Corresponding author; e-mail: rutishauser@biology.ucsc.edu.

evate metabolic rate, (ii) lower core body temperature, (iii) restrict or modify blood flow, (iv) move to a warmer environment, (v) increase activity, and (vi) increase insulation (Irving and Hart 1957; Ridgway 1972; Costa and Kooyman 1982). In the short term, however, young marine mammals will thermoregulate through elevated metabolic rate from increased activity, shivering, and nonshivering thermogenesis. This is especially important in fasting or subnourished animals, which must rely primarily on stored energy in the form of lipid to support metabolic processes (Noren et al. 2003). However, the animal must balance the use of blubber-lipid stores against thermal requirements for insulation. Tapping into the blubber layer to support the energetic demands of the animal will exacerbate any thermoregulatory costs by decreasing the insulation of the animal.

Understanding postweaning survival for any pinniped is valuable, but it may be especially important to subpolar otariids that have abbreviated lactation periods. In addition, weaning is more abrupt in Antarctic fur seals and northern fur seals (*Callorhinus ursinus*) than in all other otariids, where little or no foraging takes place before weaning (Gentry and Kooyman 1986). This could make these species more vulnerable to environmental vagaries that affect survival. With a short lactation period of 4 mo (Gentry and Kooyman 1986), Antarctic fur seals (*Arctocephalus gazella*) provide an excellent system to examine the physiological role that lipid plays in thermoregulation and the transition to independence in young marine mammals. In many fur seal and sea lion species, it is difficult or impossible to study immature animals because they do not return to the natal rookery for several years. Yearling Antarctic fur seals often return to their natal rookery (M. R. Rutishauser, personal observation), so it is possible to compare pups at weaning with yearlings to examine two important factors that affect otariid life history: lipid energy stores and thermal homeostasis.

The purpose of this study was to examine the role that lipid plays in a young aquatic homeotherm by (i) investigating the thermoregulatory response of young Antarctic fur seals, (ii) assessing the effect of body composition on the thermoregulatory abilities of Antarctic fur seal pups, and (iii) comparing the thermal responses of pups with yearling Antarctic fur seals. These data were used to produce a model of postweaning fasting capability and to predict maximum travel distances after weaning.

Material and Methods

Study Site

Fieldwork took place at Cape Shirreff, Livingston Island (62°28'S, 60°46'W), in conjunction with the U.S. Antarctic Marine Living Resources program from February 11 to 23, 1999, and February 11 to 27, 2000. Cape Shirreff extends north of Livingston Island into the Drake Passage and has a maritime

climate. Snow remains on the ground until December. The weather was typically overcast with a mean air temperature of 2.5°C. Sea surface temperatures around Cape Shirreff were approximately 1.5°C during the study periods (Martin 1998, 1999).

Animals

Twenty-four Antarctic fur seals were assessed in this study: 12 pups (seven females, five males) and 12 yearlings (six males, six females). No animal was in the study as both a pup and later as a yearling. Known-age tagged animals ($N = 17$) and untagged animals ($N = 7$) were used. Fully molted fur seal pups were taken from the rookery and held up to 24 h in ventilated boxes while data were collected. For tagged pups ($N = 11$), birth date was known by bleach-marking the pups within 2 d of birth, with subsequent addition of flipper tags before molting. Mean age of the pups when data were collected was 72.9 ± 0.7 d, ranging from 66 to 89 d. Attendance behavior of mothers was known through direct observation or equipping mothers with radio transmitters. Consequently, tagged pups could be removed from the rookery while their mothers were at sea, 2–3 d postdeparture. One anonymous pup was taken when its behavior and location suggested that its mother was at sea but was not held overnight because of the difficulty in predicting its mother's return. Nonmolting yearlings were taken opportunistically. Yearlings were identified by mass and length for untagged animals ($N = 6$) or tags placed the previous year for known animals ($N = 6$). Untagged animals were marked with bleach to prevent recapture. This work was approved by University of California, Santa Cruz, Chancellor's Animal Research Committee (permit number cost \$98.10).

Body Composition

Body composition was determined once for each subject from water space and total mass (Pace and Rathbun 1945; Costa 1987). This technique has been widely used and validated in Antarctic fur seals (Arnould et al. 1996b). Total body mass was determined to the nearest 0.5 kg by suspending the animals in a mesh bag from a hanging scale (Pesola, Baar). Water space was determined by the dilution of 1.85 MBq of tritium diluted in sterile saline to 1.0 mL and injected intraperitoneally. The isotope was allowed to equilibrate for 3 h (Costa 1987), after which a blood sample was drawn. After centrifuging the blood (5 min at 1,500 relative centrifugal force), samples of serum were frozen until analysis. Water was distilled from 0.25 mL of serum following the methods of Ortiz et al. (1978). Specific activity of tritium was determined on a liquid scintillation counter (LS 6500, Beckman Instruments, Fullerton, Calif.). Total body water (TBW) was subsequently determined from the activity and mass of the injectate, and the activity and mass of water was determined from the serum sample and was reduced

by 1.9% to correct for overestimation of TBW by tritiated water (Arnould et al. 1996b).

Arnould et al. (1996b) reported predictive equations to determine the percent of body mass in kilograms (M_b) as lipid (%TBL) for pups and adult female Antarctic fur seals; however, these were inappropriate for this study. The percent of M_b as water (%TBW) for pups in the study by Arnould et al. (1996b) covered a smaller range than this study, and the pups were much younger (1, 2, 4, and 36 d). Directly measured tissue hydration values are not available for older Antarctic fur seal pups and yearlings. However, Arnould et al. (1996b) provide the best available directly measured hydration state of lean tissue measured in this species. Hydration values were assumed to be 74.7% for pups and 70.7% for yearlings in this study, taken from pups and adult females, respectively (Arnould et al. 1996b). Lipid was assumed to have no water (Costa 1987). Using the above hydration values, the method of Pace and Rathbun (1945) was modified to calculate total body lipid:

$$\text{TBL} = M_b - 1.34 \times \text{TBW}, \quad (1)$$

where M_b is body mass (kg), TBL is total body lipid (kg), and TBW is total body water (kg). Similarly, TBL for yearlings was calculated with the following equation:

$$\text{TBL} = M_b - 1.41 \times \text{TBW}. \quad (2)$$

Lean body mass (LBM) was then calculated as the difference between M_b and TBL.

Metabolic Measurements

Metabolic rates were determined for animals resting in air and water using flow-through, indirect calorimetry. The experimental setup was modeled after that of Donohue et al. (2000). Two experimental chambers (1.0 m × 0.5 m × 0.3 m) were used, one for in-air measurements and one for in-water measurements. The chambers were covered by a plastic lid forming an airtight seal. Each lid had a window for observing the subject. The chamber was airtight with several ports for sampling air or inserting temperature probes. Three types of trials were conducted with each animal in random order: in ambient air ($5.6^\circ \pm <0.1^\circ\text{C}$), in cold water ($0.6^\circ \pm <0.1^\circ\text{C}$), and in warm water ($10.3^\circ \pm <0.1^\circ\text{C}$). Water temperatures were adjusted before each trial by the addition of ice or hot water to the chamber and measured with a calibrated, plastic-coated thermocouple (BAT-12, Physitemp Instruments, Clifton, N.J.). Temperature of the water and air were monitored and varied less than 1°C . The mean of temperatures at the start and end of a trial was used for subsequent calculations.

With the exception of age and thermal neutrality, metabolic rates were measured under standard conditions as defined by Kleiber (1975). The subjects were quiescent, awake, nonpreg-

nant, nonlactating, and postabsorptive. A postabsorptive state was obtained by fasting the animals for at least 12 h and usually overnight. This delay allowed the pups' metabolism to stabilize to a fasting condition as reported for Antarctic fur seal pups and other animals (Cherel et al. 1988; Rea and Costa 1992; Arnould et al. 2001). A visual inspection for lipemia in blood serum was also conducted to ensure a postabsorptive state. Core body temperature was recorded before and after each trial using a calibrated, plastic-coated thermocouple (BAT-12, Physitemp Instruments) inserted 16 cm into the rectum of the animal.

Animals were allowed to acclimate to the chamber for 45 min before metabolic measurements. Resting metabolic rate (RMR) in air and water was recorded for periods of quiescence 10 min or greater. Tapping on the chamber kept the animals awake during the trial to avoid measuring sleeping metabolic rates. Total time in the chamber was approximately 120 min. Following each trial, animals were maintained out of the chamber in a ventilated box for at least 60 min and until core body temperature returned to initial values.

The animals' behavior during the metabolic measurements were recorded in intervals ranging from 30 s to 2 min. Air temperature and barometric pressure were recorded every 5 min (Davis Instruments, Hayward, Calif.). Relative humidity inside the chamber was recorded every 5 min using a thermohygrometer taped to the window in the chamber lid (Oakton Instruments, Vernon Hills, Ill.). Average values for these parameters were used to correct flow rates to the STPD for dry gas.

Ambient air was drawn through the metabolic chamber with a wet/dry vacuum (Shop-Vac, Williamsport, Pa.). A sample of the outflow was scrubbed of water and carbon dioxide with 120 g of anhydrous calcium sulfate (Drierite, Xenia, Ohio) and 60 g of barium hydroxide (Baralyme, Allied Healthcare Products, St. Louis), respectively. Oxygen consumption was determined by measuring the reduction of oxygen in the sample air relative to ambient air with an oxygen analyzer (Ametek S-3A Oxygen Analyzer, Paoli, Pa.). Airflow through the chamber was measured with a flowmeter (American Meter, Horsham, Pa.) and maintained at 40 L min^{-1} . Before each trial, the system was calibrated and checked for leaks using the nitrogen dilution technique (Fedak et al. 1981). The proportion of oxygen was logged continuously on a personal computer with a sample interval of 0.5 s (Datacan V, Sable Systems International, Salt Lake City, Utah). Oxygen consumption was calculated from the data using equation (4b) from Withers (1977) with analysis software (Datacan V Software, Sable Systems International).

For these calculations, the respiratory quotient (RQ) for pups was taken from Arnould et al. (2001) based on the number of days since the mothers departure. For the one anonymous pup and all yearlings, an intermediate value of those reported by Arnould et al. (2001) of 0.75 was used for the RQ. This value is typical for a fasting mammal relying on fat metabolism

(Schmidt-Nielsen 1997). The effects of evaporative water loss from the animal were assumed to be negligible (Withers 1977).

Modeling Postweaning Energy Reserves

We developed two models, representing likely minimum and maximum fasting durations after weaning. Using data in this study and previously published values from the literature, the models were based on discrete time steps of 0.1 d. The models took the general form of

$$\%TBL(t+1) = 100 \times \frac{L(t) - MR(t)}{M(t) - MR(t)}, \quad (4)$$

where $\%TBL(t)$ is the $\%TBL$ at time t , $L(t)$ is the lipid (kg) at time t , $M(t)$ is body mass (kg) at time t , and $MR(t)$ is the amount of lipid (kg) used in 0.1 d with a mass of $M(t)$ and a $\%TBL$ of $L(t)$. Mass of lipid consumed was calculated assuming that 1 mL of oxygen consumption is equivalent to 19.7 J and that lipid contains 39.3 J gm^{-1} (Schmidt-Nielsen 1997). Percent TBL was chosen as the predicted variable because the proportional amount of TBL most likely determines the limits of fasting capability (Leiter and Marliss 1982; Goodman et al. 1984; Taylor and Konarzewski 1989), when the animal succumbs to starvation.

Some simplifying assumptions were made to produce the models. Assumptions were also made where data were lacking in this study or the literature. For example, several studies suggest that the thermal environment affects the metabolic rate of swimming animals, even though they have a metabolic rate elevated because of the energetic cost of locomotion (Feldkamp 1987; Feldkamp et al. 1989; Hind and Gurney 1997). From these studies, metabolic rates measured in the cold water treatments were assumed to be most representative of thermoregulatory effects as well as the effects of $\%TBL$ and mass. For the model of fasting capability, the multiple linear regression for metabolic rate as a function of $\%TBL$ and mass was used (Table 1). Once weaned, pups were assumed to remain at sea without hauling out or feeding.

Two models were created that likely bracket the true fasting duration of these animals. The models were derived from estimates of a maximum and minimum metabolic rates at sea. Because there are no reported values for free-ranging metabolic rates (FMR) of young otariids at sea, FMRs for nonlactating females at sea were used as a maximum metabolic rate. In addition, basal metabolic rate (BMR) predicted by Kleiber (1975) was assumed to be equivalent to RMR to ensure a maximum metabolic estimate. Using feeding rates, Perez and Mooney (1985) found that energy consumption of nonlactating Northern fur seals was 3.7 times the predicted BMR. The met-

Table 1: Multiple regression analysis of metabolic rate for ambient air, cold water, and warm water treatments in relation to mass and $\%TBL$

	Treatment		
	Cold Water	Warm Water	Air
r^2	.739	.651	.742
N	21	23	23
ANOVA:			
F ratio	25.486	39.194	37.015
P	<.001	<.001	<.001
Independent variables:			
Mass:			
t value	4.687	6.260	7.962
Coefficient	11.426	9.342	9.822
P Value	<.001	<.001	<.001
Coefficient of partial determination	.550	(.543)	(.728)
$\%TBL$:			
t value	-2.510	(-.967)	(-.186)
Coefficient	-1.765	(-.510)	(-.072)
P Value	.022	(.345)	(.854)
Coefficient of partial determination	.292	(.050)	(.238)

Note. Dependent variable is metabolic rate. Items in parentheses are for illustration only and not part of the regression (see "Discussion").

abolic rate predicted by the cold water regression (Table 1) was multiplied by 3.7 to represent a probable maximum FMR and a minimum fasting duration ($\text{model}_{\text{MR-MAX}}$). RMR in cold water from this study most likely represents a minimum FMR and a maximum fasting duration ($\text{model}_{\text{MR-MIN}}$). For simplicity, LBM was assumed to not be an energy source and, thus, remained constant after weaning. Admittedly, this underestimates the energy reserves of the animal. However, similar methods have been used to calculate fasting capability in a variety of birds (Taylor and Konarzewski 1989; Navarro 1992). Furthermore, Arnould et al. (2001) have found that protein comprises only 5% of total energy expenditure in fasting Antarctic fur seal pups; thus, the overall impact on the model is small. Energy reserves were based on initial TBL. For all models, an animal was assumed to succumb to starvation when %TBL reached the minimum found for this study (6.5%), possibly underestimating fasting capability.

Given the similar relations between metabolic rate and body mass and %TBL of pups and yearlings over a wide range of these parameters, it is likely that the metabolic rate and thermal properties of the model weaned pup is reasonably predicted by the regressions found in this study. A starting body composition and mass for a weaned pup was calculated by keeping mean %TBL constant, using the mean body mass for all pups, the mean growth rate of pups at Cape Shirreff (0.09 kg d^{-1} ; M. E. Goebel, unpublished data), and mean age at weaning of 120 d from Lunn et al. (1993) and Doidge and Croxall (1989; Fig. 1). The resulting calculations yielded a pup of 12.9 kg lean tissue and 4.1 kg lipid (31% TBL). This starting condition is larger and has a higher %TBL than other Antarctic fur seal colonies, which matches the higher growth rates and larger pups at Cape Shirreff (M. E. Goebel, unpublished data). There are no data in the literature for body composition of weaned Antarctic fur seals, so body composition was assumed to be the %TBL found in this study. If %TBL increases over the last trimester of lactation, as has been shown in Australian fur seals (*Arctocephalus pusillus doriferus*; Arnould and Hindell 2002), the model may underestimate weaned fasting capability. In addition, male and female fur seal pups have been found to have different body compositions (Arnould et al. 1996a; Beauplet et al. 2003). In order to address variation in %TBL related to sex, age, year, location, or other factors, decline in %TBL was modeled for a lean pup and a fat pup. These animals were assumed to have an identical lean body mass with %TBL one standard deviation (SD) above and below the mean. This yielded a lean pup of 12.9 kg lean tissue and 4.1 kg lipid (24% TBL) and a fat pup with 12.9 kg lean tissue and 8.0 kg lipid (38% TBL).

Statistical Analyses

SYSTAT (SPSS, version 8.0) was used for all statistical analyses. Percentage data were square root–arcsine transformed for analysis. Least-square linear regressions were calculated to analyze

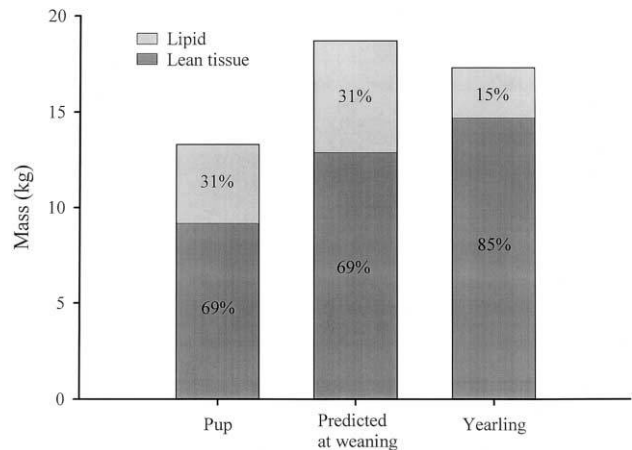


Figure 1. Mean mass and proportion of lean tissue and lipid for pups and yearlings determined by total body water. Values predicted for weaning are used in models of fasting capability. Mass and body composition for a weaned pup were calculated by keeping mean percent lipid of body mass constant, using mean mass for all pups, mean growth rate of pups at Cape Shirreff (0.09 kg d^{-1} ; M. E. Goebel, unpublished data), and mean age at weaning of 120 d from Doidge and Croxall (1989) and Lunn et al. (1993).

relationships between measured parameters. Paired *t*-tests were used to compare treatments. Age groups or sexes in the same treatment were compared using two-sample *t*-tests. Repeated-measures (RM) ANCOVA and ANOVA were used for comparisons between treatments. Non-RM ANCOVA and ANOVA were used to compare sexes and age groups in the same treatment. A Bonferroni test was used for post hoc pairwise comparisons. Interaction terms using the general linear model were used to compare slopes of relationships. A *P*-value of less than or equal to 0.05 was considered a significant difference. Means are reported \pm SEM. Coefficients of partial determination were calculated as by Neter et al. (1996).

Results

Body Composition

Males were heavier than females for each age class, and yearlings were heavier than pups for each sex (Table 2; Fig. 1). Mean mass of the pups was $15.4 \pm 0.2 \text{ kg}$ for males and $11.8 \pm 0.3 \text{ kg}$ for females ($t = -4.056$, $df = 10$, $P = 0.002$). Yearlings massed $18.9 \pm 0.5 \text{ kg}$ for males and $15.7 \pm 0.3 \text{ kg}$ for females ($t = -3.316$, $df = 10$, $P = 0.008$). Yearlings were heavier than pups for both females (Table 2; $t = -3.654$, $df = 11$, $P = 0.004$) and males ($t = -4.964$, $df = 9$, $P = 0.001$). There were no detectable differences between years for all body composition and mass measures.

For all animals, %TBW varied with mass ($r^2 = 0.867$, $N = 23$, $P < 0.001$). Yearlings had an average %TBW of $60\% \pm 2\%$ while pups had an average %TBW of $51\% \pm 2\%$.

Table 2: Summary of mean values \pm SEM for mass, %TBL (total body lipid), metabolic rates, and body temperature

	Mass (kg)	%TBL	Metabolic Rate (mL O ₂ min ⁻¹)			Body Temperature (°C)		
			Air	Warm Water	Cold Water	Air	Warm Water	Cold Water
Pups:								
Females (<i>N</i> = 7)	11.8 \pm .3	31 \pm 1	179 \pm 2	202 \pm 3	274 \pm 1	37.6 \pm <.1	37.2 \pm <.1	37.1 \pm <.1
Males (<i>N</i> = 5)	15.4 \pm .2	31 \pm 1	205 \pm 6	252 \pm 4	301 \pm 6	37.6 \pm <.1	37.4 \pm <.1	37.1 \pm <.1
All	13.3 \pm .7	31 \pm 1	190 \pm 2	223 \pm 2	286 \pm 3	37.6 \pm <.1	37.3 \pm <.1	37.1 \pm <.1
Yearlings:								
Females (<i>N</i> = 6)	15.7 \pm .3	15 \pm 1	206 \pm 4	252 \pm 3	351 \pm 3	37.5 \pm <.1	37.1 \pm <.1	36.7 \pm <.1
Males (<i>N</i> = 6)	18.9 \pm .5	15 \pm 1	253 \pm 2	273 \pm 3	380 \pm 7	37.4 \pm <.1	37.0 \pm <.1	36.5 \pm <.1
All	17.3 \pm .7	15 \pm 1	229 \pm 9	263 \pm 3	366 \pm 3	37.5 \pm <.1	37.0 \pm <.1	36.6 \pm <.1

Mean %TBL calculated from these values was identical between the sexes for pups ($t = -0.074$, $df = 9$, $P = 0.943$) and yearlings ($t = -0.178$, $df = 10$, $P = 0.862$). However, pooled values for %TBL of males and females showed that %TBL in pups was greater than in yearlings (Fig. 1; $t = 5.995$, $df = 21$, $P < 0.001$). TBL was not different between male and female pups ($t = -1.113$, $df = 9$, $P = 0.084$) or between male and female yearlings ($t = -0.872$, $df = 10$, $P = 0.404$). Unlike %TBL, pooled TBL of pups (2.6 ± 0.1 kg) was less than pooled TBL in yearlings (yearlings: 4.0 ± 0.1 kg; $t = 3.140$, $df = 21$, $P = 0.005$).

Although %TBL did not vary with mass for individual age classes (pups: $F_{1,9} = 0.250$, $P = 0.629$; yearlings: $F_{1,9} = 1.354$, $P = 0.272$), for all animals, %TBL did relate negatively to mass driven by the tendency of yearlings to be leaner and heavier than pups ($r^2 = 0.258$, $N = 23$, $P = 0.013$). TBL tended to increase with mass for pups but was not significant ($r^2 = 0.222$, $F_{1,9} = 4.409$, $P = 0.065$). TBL was positively related for yearlings ($r^2 = 0.335$, $N = 11$, $P = 0.049$). In contrast to %TBL, TBL of all animals did not relate to mass ($F_{1,21} = 0.037$, $P = 0.849$).

Mean age of all pups was 72.9 ± 0.7 d with no difference between sexes ($t = 1.166$, $df = 9$, $P = 0.264$). Age of the pups did not correlate with mass, %TBL, TBL, %LBM (percent of mass as lean tissue), and LBM ($P > 0.05$).

Body Temperatures

There was no difference in body temperature between males and females in any treatment for pups and yearlings or between years ($P > 0.05$); therefore, years and sexes were combined for analysis. For animals resting in air, mean body temperature did not differ between pups and yearlings ($t = 0.847$, $df = 22$, $P = 0.406$) and was $37.5^\circ \pm <0.1^\circ\text{C}$ for all animals combined. This contrasted with animals resting in water. Mean body temperature for pups in warm water was $37.3^\circ \pm <0.1^\circ\text{C}$ and was higher ($t = 2.350$, $df = 20$, $P = 0.029$) than for yearlings ($37.0^\circ \pm <0.1^\circ\text{C}$). Similarly, mean body temperature for pups in cold water ($37.1^\circ \pm <0.1^\circ\text{C}$) was higher ($t = 2.917$, $df =$

21, $P = 0.008$) than for yearlings in cold water ($36.6^\circ \pm <0.1^\circ\text{C}$; Table 2). Body temperatures were different between treatments for pups and yearlings (yearlings: RM ANOVA $F_{2,9} = 19.508$, $P < 0.001$; pups: RM ANOVA $F_{2,11} = 15.097$, $P < 0.001$) and for all pairwise combinations ($P < 0.03$). However, there was no relation between body temperature measured in air and air temperature ($F_{1,22} = 0.167$, $P = 0.167$) for combined pups and yearlings.

Body temperature showed a relation with %TBL in cold water treatments for combined pups and yearlings ($BT_0 = 0.025\%TBL + 36.289$, $r^2 = 0.361$, $N = 22$, $P = 0.003$) but was not significant for other treatments ($P < 0.05$; Fig. 2). Although we found a difference between mean body temperatures for pups and yearlings in water treatments, ANCOVA with %TBL as a covariate revealed no difference between groups ($F_{1,19} = 1.149$, $P = 0.297$).

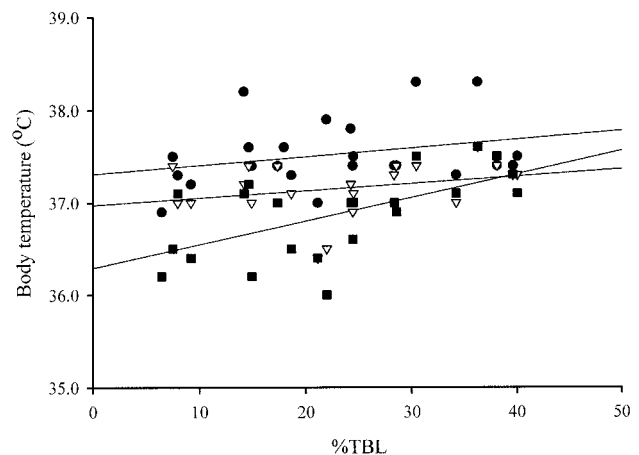


Figure 2. Relationships between percent lipid of body mass (%TBL) and body temperature for Antarctic fur seal pups and yearlings in air with a mean temperature of $5.6^\circ \pm <0.1^\circ\text{C}$ (filled circle), warm water with a mean temperature of $10.3^\circ \pm <0.1^\circ\text{C}$ (open triangle), and cold water with a mean temperature of $0.6^\circ \pm <0.1^\circ\text{C}$ (filled square). The regression for cold water is $y = 0.026x + 36.3$ ($r^2 = 0.36$, $P = 0.003$). The regressions for other treatments are not significant ($P > 0.05$). Data for pups and yearlings are combined.

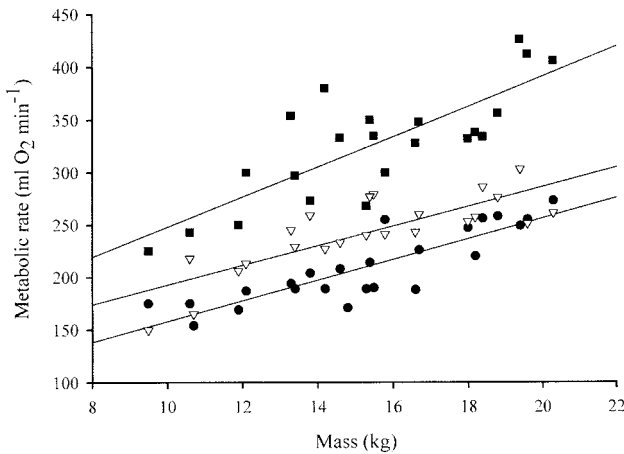


Figure 3. Relationships between body mass and metabolic rate for Antarctic fur seal pups and yearlings in air with a mean temperature of $5.6^{\circ} \pm <0.1^{\circ}\text{C}$ (filled circle), warm water with a mean temperature of $10.3^{\circ} \pm <0.1^{\circ}\text{C}$ (open triangle), and cold water with a mean temperature of $0.6^{\circ} \pm <0.1^{\circ}\text{C}$ (filled square). Data are combined for pups and yearlings. The regression for air treatments is $y = 9.82x + 59.7$ ($r^2 = 0.74$, $P < 0.001$); the regression for warm water treatments is $y = 9.34x + 99.5$ ($r^2 = 0.65$, $P < 0.001$); and the regression for cold water treatments is $y = 14.3x + 105$ ($r^2 = 0.63$, $P < 0.001$).

Metabolic Rates

Mean RMR in air for combined pups and yearlings was 210 ± 37 mL O_2 min^{-1} with a combined mean mass of 15.3 ± 0.1 kg. Log-log regression produced a predictive equation ($\text{RMR}_{\text{air}} = 30.0 M^{0.72}$, $N = 24$, $P = 0.003$, $r^2 = 0.73$). Mean RMR for all animals in cold water was 326 ± 53 mL O_2 min^{-1} and 242 ± 36 mL O_2 min^{-1} in warm water. There were no detectable differences between years; thus, 1998 and 1999 data were combined.

In general, metabolic rates increased with body mass (Fig. 3). Linear regressions between sex and age class were not different ($P > 0.05$ for all coefficients) and were combined for analysis. An exception was the metabolic rates measured for yearlings and pups in warm water; these had different slopes (ANCOVA, $F_{1,19} = 4.843$, $P = 0.04$). Although yearling metabolic rates in warm water did not show a relation to body mass ($F_{1,9} = 1.245$, $P = 0.245$), metabolic rate of pups in warm water were related to mass ($r^2 = 0.688$, $F_{1,9} = 15.091$, $P = 0.004$). Linear regressions for pups and yearlings were not significantly different for metabolic rate, and all parameters of body composition (body mass, %TBL, TBL, %LBM, and LBM) within treatments ($P > 0.05$). The one exception was for the relation between body mass and metabolic rate in warm water. Given the other nonsignificant results, this exception was assumed to be caused by sampling error. Thus, yearling and pup data were combined for analysis of metabolic rates.

Body mass explained some of the variation in metabolic rates for metabolic treatments in warm water, ($r^2 = 0.651$, $F_{1,21} =$

39.194 , $P < 0.001$), cold water ($r^2 = 0.636$, $F_{1,20} = 34.937$, $P < 0.001$), and air ($r^2 = 0.742$, $F_{1,21} = 74.955$, $P < 0.001$). The coefficient of variation for the relation between metabolic rate and body mass in cold water was different from the coefficients of variation for air ($F_{1,40} = 4.463$, $P = 0.041$) but not for warm water. There was no relation between metabolic rate and air temperatures experienced by pups and yearlings combined (0.8° – 5.6°C , $F_{1,22} = 3.294$, $P = 0.083$).

Metabolic rates decreased with %TBL for all treatments (Fig. 4). Linear regressions were not different between sexes and age classes ($P > 0.05$ for all coefficients) and were combined for analysis. For animals resting in air, metabolic rate was related to %TBL ($r^2 = 0.218$, $F_{1,21} = 5.850$, $P = 0.025$), as well as for animals in warm water ($r^2 = 0.275$, $F_{1,20} = 7.582$, $P = 0.012$) and cold water ($r^2 = 0.421$, $F_{1,19} = 13.787$, $P = 0.001$).

Metabolic rates for pups and yearlings were not different when compared with %TBL and body mass as covariates in cold water ($F_{1,17} = 0.698$, $P = 0.415$), warm water ($F_{1,18} = 0.671$, $P = 0.423$), and air ($F_{1,19} = 1.161$, $P = 0.295$). With both mass and %TBL as covariates, different metabolic rates were found between treatments for combined pup and yearling data (RM ANCOVA, $F_{2,66} = 132.528$, $P < 0.001$). Pairwise comparisons were different between all treatments (post hoc Bonferroni, $P < 0.001$).

Postweaning Model

Model_{MR-MAX} predicted a minimum fasting capability ranging from 6.6 to 13.8 d with a mean %TBL giving 9.8 d until suc-

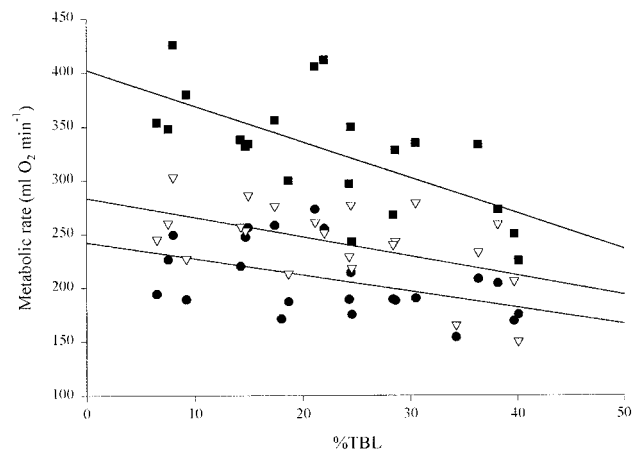


Figure 4. Relationships between percent lipid of body mass (%TBL) and metabolic rate for Antarctic fur seal pups and yearlings in air with a mean temperature of $5.6^{\circ} \pm <0.1^{\circ}\text{C}$ (filled circle), warm water with a mean temperature of $10.3^{\circ} \pm <0.1^{\circ}\text{C}$ (open triangle), and cold water with a mean temperature of $0.6^{\circ} \pm <0.1^{\circ}\text{C}$ (filled square). Data are combined for pups and yearlings. The regression for air treatments is $y = -3.33x + 402$ ($r^2 = 0.42$, $P = 0.001$); the regression for warm water treatments is $y = -1.80x + 283$ ($r^2 = 0.28$, $P = 0.012$); and the regression for cold water treatments is $y = -1.51x + 242$ ($r^2 = 0.22$, $P = 0.025$).

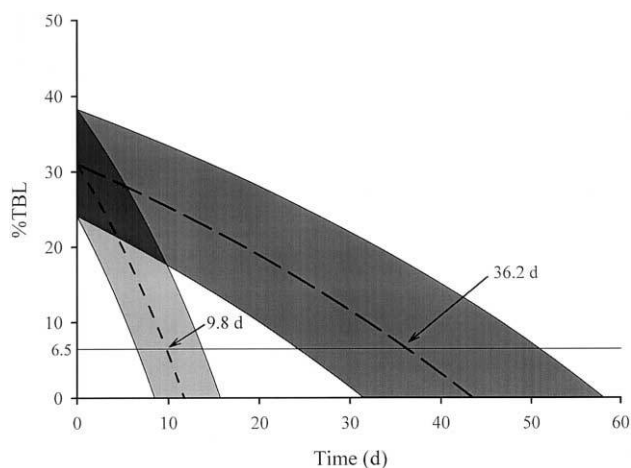


Figure 5. Decrease in percent lipid of body mass (%TBL) for a weaned Antarctic fur seal as predicted by model_{MR-MAX} (small dashed line) and model_{MR-MIN} (large dashed line). Mass at weaning is estimated to be 18.7 kg with 31% lipid (small dashed line). Shaded areas represent ± 1 SD %TBL while keeping lean body mass constant. Death is assumed to occur at or below 6.5% TBL (large dashed line). Model_{MR-MAX} had an initial rate of mass loss of $2.9\% \text{ d}^{-1}$ while model_{MR-MIN} had an initial rate of $0.7\% \text{ d}^{-1}$.

cumbing to starvation. Model_{MR-MIN} ranged from 24.3 to 50.9 d with a mean %TBL yielding 36.2 d (Fig. 5). Mass loss in model_{MR-MAX} increased from 2.9% to 3.4% d^{-1} for an average %TBL. Model_{MR-MIN} had a nearly constant rate of mass loss, ranging from 0.8% to 0.9% d^{-1} .

Discussion

Metabolic Rates and Thermoregulation

In view of the changes in metabolic rate and core body temperature, young Antarctic fur seals appear to live outside their thermal neutral zone (TNZ) while at sea. Body temperature and metabolic rate did not vary over a range of air temperatures from 0.8° to 5.6°C , indicating the animals were thermally neutral in air. In contrast, metabolic rate of young Antarctic fur seals increased when exposed to both warm and cold water. Using the methods of Scholander et al. (1950), these changes in metabolic rate indicate a lower critical temperature (T_{lc}) of 14.4°C (Fig. 6). Based on Newtonian cooling, this method also estimates a body temperature reasonably close to the measured value from this study, which lends support to the predicted T_{lc} . However, Antarctic fur seal pups and yearlings live in waters that are well below this temperature. Mean sea surface temperature varies from 0° to 5°C in the breeding range of Antarctic fur seals (Riedman 1990; Orsi et al. 1995). Even at their maximum reported range in Tierra del Fuego (Payne 1979; Orsi et al. 1995), sea surface temperature is only 12°C , 2°C colder than the animals T_{lc} . As a result, immature Antarctic fur seals have a higher metabolic overhead while at sea than would be pre-

dicted by allometric relationships or from studies of resting metabolism under standard conditions for young animals. This has important implications for calculations of food consumption for individuals or estimates of trophic level interactions (Boyd 2002). These results for Antarctic fur seals are not unique for marine mammals, especially otariids and smaller species. For example, adult California seal lions (*Zalophus californianus*) routinely live in water that is near their T_{lc} (Liao 1990). Sea otters (*Enhydra lutris*), the smallest marine mammal, live outside their thermal neutral zone, using activity and the heat increment of feeding to maintain thermal homeostasis (Costa and Kooyman 1984).

A labile body temperature also appears to be part of the thermoregulatory response of immature Antarctic fur seals. By lowering body temperature, the rate of heat loss is reduced because of a smaller temperature gradient between the body and the environment (Scholander et al. 1950; Hart 1971). This thermoregulatory mechanism occurs in other aquatic mammals living in thermally challenging environments. The Australian water rat (*Hydromys chrysogaster*; Dawson and Fanning 1981), sea otter (*Enhydra lutris*; Costa and Kooyman 1984), and North American mink (*Mustela vison*; Williams 1986) have been shown to lower body temperature and reduce the temperature gradient.

In contrast, northern fur seals appear to have a greater thermal tolerance to cold water and are able to live within their

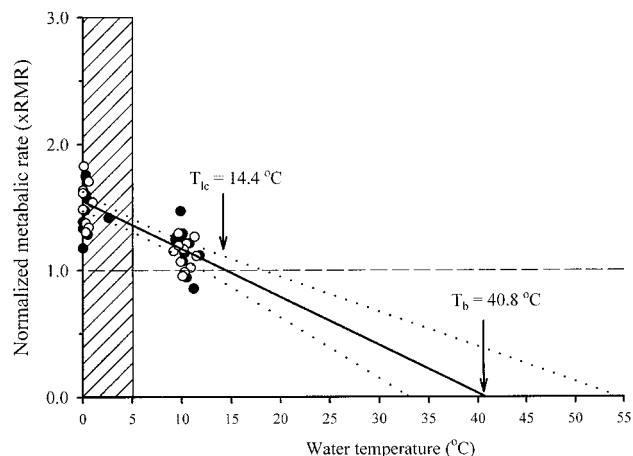


Figure 6. Relationship between water temperature and normalized metabolic rate for pups (filled circle) and yearlings (open circle). Metabolic rates were normalized to resting metabolic rate in air for each animal. Regression line (solid line) and 95% confidence interval (dotted line) are for combined data ($y = -0.038x + 1.549$, $r^2 = 0.55$, $P < 0.001$). The regression line intercepts a normalized metabolic rate of 1.0 (dashed line) at the approximate lower critical temperature (T_{lc}) and intercepts the X-axis at an estimate of body temperature (T_b). The cross-hatched area indicates water temperatures in the breeding range of the species. Intercepts and coefficients were not different between pups and yearlings for a similar regression ($P > 0.5$) nor were metabolic rates in warm and cold water treatments ($P > 0.4$).

TNZ when at sea. Northern fur seal pups (*Callorhinus ursinus*) live in a high-latitude, seasonal environment similar to that in which Antarctic fur seals live (Gentry and Kooyman 1986). Yet, postmolt northern fur seal pups show no changes in body temperatures or metabolic rates when exposed to 5°, 10°, and 20°C water (Donohue et al. 2000). Because %TBL and body mass for postmolt pups in this study and that of Donohue et al. (2000) were similar (33% TBL and 14.8 kg), it is unlikely that body composition was a factor in the different thermal response between the species. Furthermore, different metabolic capacities cannot account for these differences. Northern fur seal pups (Donohue et al. 2000) and Antarctic fur seal pups (Arnould et al. 2001; this study) have RMRs in air 2.6 and 2.3 times Kleiber's (1975) predicted value, respectively. Rather, differences in fur, blubber, or physiology may be responsible, arising from dissimilar evolutionary histories (Berta 2002).

Body Composition

In young Antarctic fur seals, both mass and %TBL affect thermoregulation (Figs. 3, 4). In cold water, %TBL and mass are the best predictors of metabolic rate, with mass accounting for most of the variation in the data. This agrees with Rea and

Costa (1992), who suggest that lipid would affect metabolic rate indirectly as an insulator. In both air and warm water, mass alone best predicted metabolic rate. Values for %TBL in Table 1 are from a multiple linear regression that included both mass and %TBL. Values of %TBL are included for illustration only because %TBL has a nonsignificant coefficient. The coefficient for %TBL in the models progresses closer to 0 as the treatments become less thermally challenging. These differences between linear regressions support Aarseth et al.'s (1999) conclusion that blubber gives little direct contribution to basal metabolic rate in marine mammals. It should be noted, however, that LBM was not the best predictor in the above models. This may be due to the negative correlation of LBM and %TBL in these data ($r^2 = 0.628$), while mass and %TBL were only weakly correlated ($r^2 = 0.258$). Fur may also complicate this relationship because fur is a good light-weight insulator but metabolically inert.

Pups in this study had %TBL higher than Antarctic fur seal pups of comparable mass from South Georgia (20%, Arnould et al. 1996a; 19%, Arnould et al. 2001). The difference could be due to geographic or interannual variation in maternal investment or pup age. Differences in weather may also play a role because thermally challenging conditions for the pups may

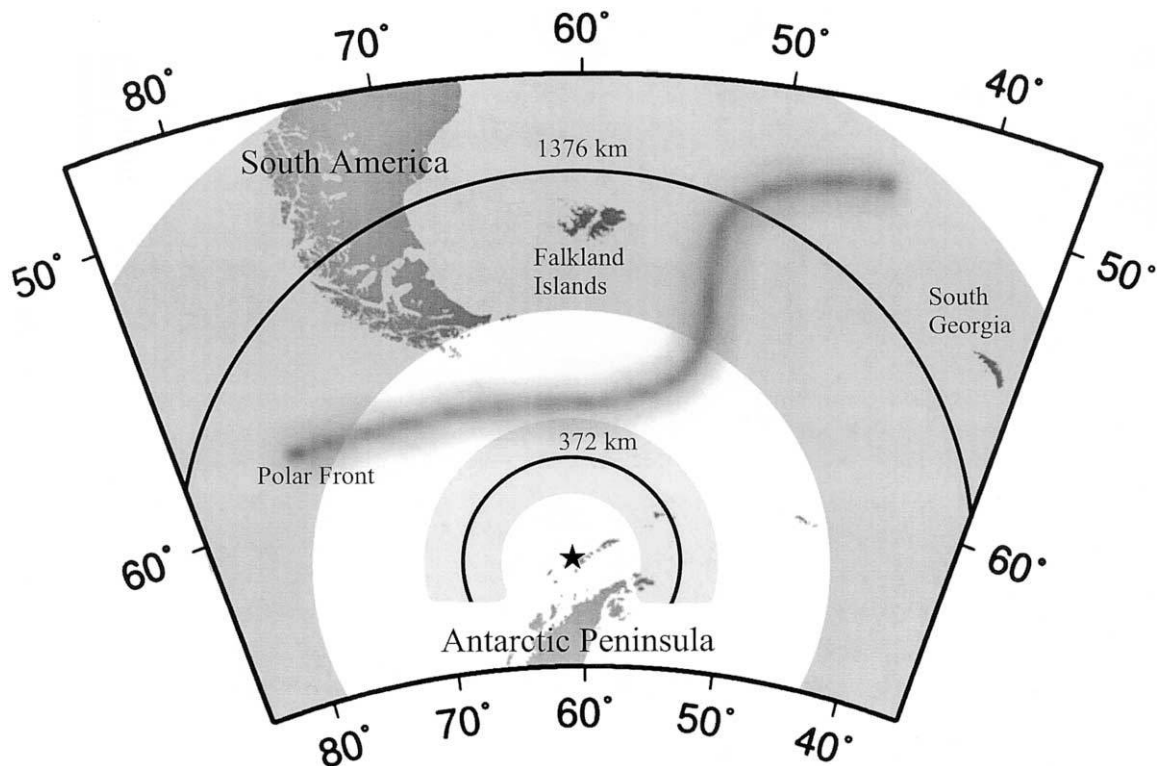


Figure 7. Predicted range of travel for a weaned Antarctic fur seal leaving Cape Shirreff (*star*) for model_{MR-MAX} and model_{MR-MIN}. The weaned pup is assumed to travel 38 km d⁻¹ and succumb to starvation at 6.5% total body lipid (TBL). Mass and body composition at weaning is 18.7 kg and 31% TBL, respectively (Fig. 2). Shaded areas represent ± 1 SD %TBL while keeping lean body mass constant. The location of the polar front is approximate and varies annually.

require reallocation of energy away from growth to thermo-regulation. Pup age and body composition were not related as shown by Arnould et al. (1996a), likely because of the small age range of pups in this study. Yearlings from this study had %TBL similar to adult female Antarctic fur seals (11.2%, Arnould 1995; 14.5%, Arnould et al. 1996b) and territorial male Antarctic fur seals (13%–21%, Boyd and Duck 1991). From a thermal perspective, yearlings would benefit from larger lipid stores. However, the similarity to adult values suggests buoyancy (Webb et al. 1998; Skrovan et al. 1999; Williams et al. 2000) or streamlining (Ryg et al. 1988) may determine the limit to %TBL. Alternatively, foraging efficiency and rate of caloric intake may limit %TBL as well.

Implications for Postweaning Foraging and Survival

Lipid energy reserves of a weaned Antarctic fur seal pup are a finite resource that must support metabolic demands of the animal until successful foraging occurs. Model_{MR-MAX} predicted rates of mass loss of 2.9%–3.9% d⁻¹, similar to values from the literature for fasting pups while onshore. Rates of mass loss for postabsorptive Antarctic fur seals pups during maternal foraging trips have been reported from 2.7% to 4.9% d⁻¹ (Arnould et al. 1996a, 2001; Guinet et al. 2000). In Steller sea lions (*Eumetopias jubatus*), 20-kg pups live for an average of 11 d after birth if their mother abandons them (Brandon 2000). Six-week-old Steller sea lions lose body mass at a rate of 2.5% d⁻¹ (Rea et al. 2000). Model_{MR-MIN} predicted mass loss at 0.7%–0.8% d⁻¹, much lower than that for fasting pups on shore. Assuming that rates of fasting mass loss at sea are greater than rates onshore reported in the above studies, the best estimate is close to model_{MR-MAX} and the models reasonably bracket the mean number of days an Antarctic fur seal can fast after weaning.

Using physiological data and a simple model, we made a prediction of the distribution of young Antarctic fur seals, addressing a fundamental question of ecology (Begon and Mortimer 1986). The metabolic relations presented in this study suggest that moving to warmer water would reduce the costs of thermoregulation. The polar front and the subantarctic front may be such destinations that reduce thermoregulatory costs because water warms from 2° to 5°C at the polar front and from 5° to 8°C at the subantarctic front (Orsi et al. 1995). Ragen et al. (1995) found that the average sustained rate of travel after weaning in northern fur seal pups was 38 km d⁻¹ (0.44 m s⁻¹). Given this rate and the fasting capabilities from the models, we find Antarctic fur seals could travel between 372 and 1,376 km with an average body composition (Fig. 7). These values bracket the maximum estimated foraging range for a lactating Antarctic fur seal from Kerguelen Island, which is 650 km (Guinet et al. 2001). The polar front or the subantarctic front is a likely destination for fur seals, where they would find warmer water temperatures (Orsi et al. 1995) or

prey associated with frontal zones (Olson et al. 1994). With the shorter distance as a more reasonable travel estimate, the polar front is within the estimated travel range of only the most well-provisioned pups (>1 SD %TBL). However, the lipid stores of nearly all young fur seals are adequate to reach feeding grounds used by adult females during the breeding season (Martin 1998, 1999; Goebel et al. 2000). In one possible scenario based on these models, weaned fur seals feed in areas used by females and then travel to the polar front or the subantarctic front. Consequently, food resources near natal rookeries may serve as a critical resource to ensure the survival of weaned animals.

Acknowledgments

Special thanks to the members of the Antarctic Marine Living Resources (AMLR) Program team at Southwest Fisheries Science Center (SWFSC), La Jolla, California. This work was made possible by the hardworking field crew at Cape Shirreff: Dr. Rennie Holt (program director of the US-AMLR program), Mike Taft, Dr. Wayne Trivelpiece, Brian Parker, and Terry Carsten (SWFSC). We gratefully received help from the neighboring Instituto Antártico Chileno field camp, consisting of Veronica Vallejos, Olivia Blank, Layla Osmund, Jorge Acevedo, and Mario Brione. The US-AMLR program and Antarctic Support Associates provided logistical support for this work. Funding was provided by the National Science Foundation Office of Polar Programs (OPP-9726567), the Department of Biology at University of California, Santa Cruz, and the Meyers Foundation.

Literature Cited

- Aarseth J.J., E.S. Nordøy, and A.S. Blix. 1999. The effect of body fat on basal metabolic rate in adult harp seals (*Phoca groenlandica*). *Comp Biochem Physiol* 124A:69–72.
- Arnould J.P.Y. 1995. Indices of body condition and body composition in female antarctic fur seals (*Arctocephalus gazella*). *Mar Mamm Sci* 11:301–313.
- Arnould J.P.Y., I.L. Boyd, and D.G. Socha. 1996a. Milk composition and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups. *Can J Zool* 74:254–266.
- Arnould J.P.Y., I.L. Boyd, and J.R. Speakman. 1996b. Measuring the body composition of Antarctic fur seals (*Arctocephalus gazella*): validation of hydrogen isotope dilution. *Physiol Zool* 69:93–116.
- Arnould J.P.Y., J.A. Green, and D.R. Rawlins. 2001. Fasting metabolism in Antarctic fur seal (*Arctocephalus gazella*) pups. *Comp Biochem Physiol* 129A:829–841.
- Arnould J.P.Y. and M.A. Hindell. 2002. Milk consumption, body composition, and pre-weaning growth rates of Austra-

- lian fur seal (*Arctocephalus pusillus doriferus*) pups. *J Zool (Lond)* 256:351–359.
- Baker J.D. and C.W. Fowler. 1992. Pup weight and survival of northern fur seals *Callorhinus ursinus*. *J Zool (Lond)* 227: 231–238.
- Beauplet G., C. Guinet, and J.P.Y. Arnould. 2003. Body composition changes, metabolic fuel use, and energy expenditure during extended fasting in Subantarctic fur seals (*Arctocephalus tropicalis*) pups at Amsterdam Island. *Physiol Biochem Zool* 76:262–270.
- Begon M. and M. Mortimer. 1986. *Population Ecology: A Unified Study of Animals and Plants*. 2d ed. Sinauer, Sunderland, Mass.
- Berta A. 2002. Pinniped evolution. Pp. 921–929 in W.F. Perrin, B. Würsig, and J.G.M. Thewissen, eds. *Encyclopedia of Marine Mammals*. Academic Press, San Diego, Calif.
- Blueweiss L., H. Fox, V. Kudzma, D. Nakashima, R. Peters, and S. Sams. 1978. Relationships between body size and some life history parameters. *Oecologia* 37:257–272.
- Boyd I.L. 2002. Estimating food consumption of marine predators: Antarctic fur seals and macaroni penguins. *J Appl Ecol* 39:103–119.
- Boyd I.L. and C.D. Duck. 1991. Mass changes and metabolism in territorial male Antarctic fur seals (*Arctocephalus gazella*). *Physiol Zool* 64:375–392.
- Brandon E.A.A. 2000. *Maternal Investment in Steller Sea Lions in Alaska*. PhD diss. Texas A&M University, Galveston.
- Bryden M.M. 1968. Growth and function of the subcutaneous fat of the elephant seal. *Nature* 220:597–599.
- Burns J.M. 1999. The development of diving behavior in juvenile Weddell seals: pushing physiological limits in order to survive. *Can J Zool* 77:737–747.
- Burns J.M. and M.A. Castellini. 1996. Physiological and behavioral determinants of the aerobic dive limit in Weddell seal (*Leptonychotes weddellii*) pups. *Comp Biochem Physiol* 166B:473–483.
- Cherel Y., J.C. Stahl, and Y. Le Maho. 1988. Physiology and biochemistry of long-term fasting in birds. *Can J Zool* 66: 159–166.
- Costa D.P. 1987. Isotopic methods for quantifying energy and material intake of free ranging marine mammals. Pp. 43–66 in A.C. Huntley, D.P. Costa, G.A.J. Worthy, and M.A. Castellini, eds. *Approaches to Marine Mammal Energetics*. Allen, Lawrence, Kans.
- Costa D.P. and R.L. Gentry. 1986. Free ranging energetics of northern fur seals, *Callorhinus ursinus*. Pp. 79–101 in R.L. Gentry and G.L. Kooyman, eds. *Fur Seals: Maternal Strategies on Land and at Sea*. Princeton University Press, Princeton, N.J.
- Costa D.P. and G.L. Kooyman. 1982. Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*. *Can J Zool* 60:2761–2767.
- . 1984. Contribution of specific dynamic action to heat balance and thermoregulation in the sea otter (*Enhydra lutris*). *Physiol Zool* 57:199–203.
- Craig M.P. and T.J. Ragen. 1999. Body size, survival, and decline of juvenile monk seals, *Monachus schauinslandi*. *Mar Mamm Sci* 15:786–809.
- Dawson T.J. and F.D. Fanning. 1981. Thermal and energetic problems of semiaquatic mammals: a study of the Australian water rat, including comparisons with the platypus. *Physiol Zool* 54:285–296.
- Doidge D.W. and J.P. Croxall. 1989. Factors affecting weaning weight in Antarctic fur seals *Arctocephalus gazella* at South Georgia. *Polar Biol* 9:155–160.
- Donohue M.J., D.P. Costa, M.E. Goebel, and J.D. Baker. 2000. The ontogeny of metabolic rate and thermoregulatory capabilities of northern fur seal, *Callorhinus ursinus*, pups in air and water. *J Exp Biol* 203:1003–1016.
- Fedak M.A., L. Rome, and H.J. Seeherman. 1981. One-step N₂ dilution technique for calibrating open circuit $\dot{V}O_2$ measuring systems. *J Appl Physiol* 51:772–776.
- Feldkamp S.D. 1987. Swimming in the California sea lion: morphometrics, drag, and energetics. *Mar Mamm Sci* 131:117–135.
- Feldkamp S.D., D.P. Costa, and G.K. DeKrey. 1989. Energetic and behavioral effects of net entanglement on juvenile northern fur seals, *Callorhinus ursinus*. *Fish Bull* 87:85–94.
- Gentry R.L. and G.L. Kooyman. 1986. Introduction. Pp. 3–27 in R.L. Gentry and G.L. Kooyman, eds. *Fur Seals: Maternal Strategies on Land and at Sea*. Princeton University Press, Princeton, N.J.
- Goebel M.E., D.P. Costa, D.E. Crocker, J.T. Sterling, and D.A. Demer. 2000. Foraging ranges and dive patterns in relation to bathymetry and time-of-day of Antarctic fur seals, Cape Shirreff, Livingston Island, Antarctica. Pp. 47–50 in W. Davison, C. Howard-Williams, and P. Broady, eds. *Antarctic Ecosystems: Models for Wider Ecological Understanding*. New Zealand Natural Sciences, Christchurch.
- Goodman M.N., B. Lowell, E. Belur, and N.B. Ruderman. 1984. Sites of protein conservation and loss during starvation: influence of adiposity. *Am J Physiol* 246:383–390.
- Guinet C., L. Dubroca, M.A. Lea, S. Goldsworthy, Y. Cherel, G. Duhamel, F. Bonadonna, and J.P. Donnay. 2001. Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Mar Ecol Prog Ser* 219:251–264.
- Guinet C., M. Lea, and S.D. Goldsworthy. 2000. Mass change in Antarctic fur seal (*Arctocephalus gazella*) pups in relation to maternal characteristics at the Kerguelen Islands. *Can J Zool* 78:476–483.
- Hart J.S. 1971. Rodents. Pp. 1–49 in G.C. Whittow, ed. *Comparative Physiology of Thermoregulation*. Vol. 2. Academic Press, New York.
- Higgins L.V., D.P. Costa, A.C. Huntley, and B.J. LeBoeuf. 1988.

- Behavioral and physiological measurements of maternal investment in the Steller sea lion, *Eumetopias jubatus*. *Mar Mamm Sci* 4:44–58.
- Hind A.T. and W.S.C. Gurney. 1997. The metabolic cost of swimming in marine homeotherms. *Mar Mamm Sci* 200: 531–542.
- Hindell M.A. 1991. Some life-history parameters of a declining population of southern elephant seals, *Mirounga leonina*. *J Anim Ecol* 60:119–134.
- Hindell M.A., B.J. McConnell, M.A. Fedak, D.J. Slip, H.R. Burton, P.J.H. Reijnders, and C.R. McMahon. 1999. Environmental and physiological determinants of successful foraging by naïve southern elephant seal pups during their first trip to sea. *Can J Zool* 77:1807–1821.
- Hood W.R. and K.A. Ono. 1997. Variation in maternal attendance patterns and pup behavior in a declining population of Steller sea lions (*Eumetopias jubatus*). *Can J Zool* 75:1241–1246.
- Irving L. and J.S. Hart. 1957. The metabolism and insulation of seals as bare-skinned mammals in cold water. *Can J Zool* 35:497–511.
- Kleiber M. 1975. *The Fire of Life: An Introduction to Animal Energetics*. 2d ed. Wiley, New York.
- Kooyman G.L., M.A. Castellini, R.W. Davis, and R.A. Maue. 1983. Aerobic diving limits of immature Weddell seals. *J Comp Physiol* 151:171–174.
- Lea M. and M.A. Hindell. 1997. Pup growth and maternal care in New Zealand fur seals, *Arctocephalus forsteri*, at Maatsuyk Island, Tasmania. *Wildl Res* 24:307–318.
- Leiter L.A. and E.B. Marliss. 1982. Survival during fasting may depend on fat as well as protein stores. *J Am Med Assoc* 248:2306–2307.
- Liao J.A. 1990. An Investigation of the Effect of Water Temperature on the Metabolic Rate of the California Sea Lion (*Zalophus californianus*). MS thesis. University of California, Santa Cruz.
- Lunn N.J., I.L. Boyd, T. Barton, and J.P. Croxall. 1993. Factors affecting the growth rate and mass at weaning of Antarctic fur seals at Bird Island, South Georgia. *J Mammal* 74:908–919.
- Martin J. 1998. AMLR 1997/98 Field Season Report: Objectives, Accomplishments, and Tentative Conclusions. NOAA, Southwest Fisheries Science Center, Antarctic Ecosystem Research Group. LJ-98-07.
- . 1999. AMLR 1998/99 Field Season Report: Objectives, Accomplishments, and Tentative Conclusions. NOAA, Southwest Fisheries Science Center, Antarctic Ecosystem Research Group. LJ-99-10.
- McMahon C.R., H.R. Burton, and M.N. Bester. 2000. Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarct Sci* 12: 149–153.
- Navarro R.A. 1992. Body composition, fat reserves, and fasting capability of Cape Gannet chicks. *Wilson Bull* 104:644–655.
- Neter J., M.H. Kutner, C.J. Nachtsheim, and W. Wasserman. 1996. *Applied Linear Statistical Models*. 4th ed. Irwin, Chicago.
- Noren D.P., D.E. Crocker, T.M. Williams, and D.P. Costa. 2003. Energy reserve utilization in northern elephant seal (*Mirounga angustirostris*) pups during the postweaning fast: size does matter. *J Comp Physiol* 173B:443–454.
- Olson D.B., G.L. Hitchcock, A.J. Mariano, C.J. Ashjian, G. Peng, R.W. Nero, and G.P. Podestá. 1994. Life on the edge: marine life and fronts. *Oceanography* 7:52–60.
- Orsi A.H., T. Whitworth, and W.D. Nowlin. 1995. On the meridional extent and fronts of the Antarctic circumpolar current. *Deep-Sea Res* 42:641–673.
- Ortiz C.L., D.P. Costa, and B.J. LeBoeuf. 1978. Water and energy influx in elephant seal pups fasting under natural conditions. *Physiol Zool* 51:166–178.
- Ortiz C.L., B.J. LeBoeuf, and D.P. Costa. 1984. Milk intake of elephant seal (*Mirounga angustirostris*) pups: an index of parental investment. *Am Nat* 124:416–422.
- Pace N. and E.N. Rathbun. 1945. Studies on body composition. III. The body water and chemically combined nitrogen content in relation to fat content. *J Biol Chem* 158:685–691.
- Payne M.R. 1979. Fur seals *Arctocephalus tropicalis* and *A. gazella* crossing the Antarctic convergence at South Georgia. *Mammalia* 43:93–101.
- Perez M.A. and E.E. Mooney. 1986. Increased food and energy consumption of lactating northern fur seals, *Callorhinus ursinus*. *Fish Bull* 84:371–381.
- Ragen T.J., G.A. Antonellis, and M. Kiyota. 1995. Early migration of northern fur seal pups from St. Paul Island, Alaska. *J Mammal* 76:1137–1148.
- Rea L.D. and D.P. Costa. 1992. Changes in standard metabolism during long-term fasting in northern elephant seal pups (*Mirounga angustirostris*). *Physiol Zool* 65:97–111.
- Rea L.D., D.A.S. Rosen, and A.W. Trites. 2000. Metabolic response to fasting in 6-week-old Steller sea lion pups (*Eumetopias jubatus*). *Can J Zool* 78:890–894.
- Ridgway S.H. 1972. Homeostasis in the aquatic environment. Pp. 690–747 in S.H. Ridgway and S. Charles, eds. *Mammals of the Sea*. Thomas, Springfield, Mass.
- Riedman M. 1990. *The Pinnipeds: Seals, Sea Lions, and Walruses*. University of California Press, Berkeley.
- Ryg M., T.G. Smith, and N.A. Oritsland. 1988. Thermal significance of the topographical distribution of blubber in ringed seals (*Phoca hispida*). *Can J Fish Aquat Sci* 45:985–992.
- Schmidt-Nielsen K. 1997. *Animal Physiology: Adaptation and Environment*. Cambridge University Press, Cambridge.
- Scholander P.F., R. Hock, V. Walters, F. Johnson, and L. Irving. 1950. Heat regulation in some tropical mammals and birds. *Biol Bull* 99:237–258.

- Skrovan R.C., T.M. Williams, P.S. Berry, P.W. Moore, and R.W. Davis. 1999. The diving physiology of bottlenose dolphins (*Tursiops truncatus*). II. Biomechanics and changes in buoyancy at depth. *Mar Mamm Sci* 202:2749–2761.
- Stewart R.E.A. and D.M. Lavigne. 1980. Neonatal growth of northwest Atlantic harp seals. *Pagophilis groenlandicus*. *J Mammal* 61:670–680.
- Taylor J.R.E. and M. Konarzewski. 1989. On the importance of fat reserves for the little auk (*Alle alle*) chicks. *Oecologia* 81:551–558.
- Webb P.M., D.E. Crocker, S.B. Blackwell, D.P. Costa, and B.J. LeBoeuf. 1998. Effects of buoyancy on the diving behaviour of northern elephant seals. *J Exp Biol* 201:2349–2358.
- Williams T.M. 1986. Thermoregulation of the North American mink during rest and activity in the aquatic environment. *Physiol Zool* 59:293–305.
- Williams T.M., R.W. Davis, L.A. Fuiman, J. Francis, B.J. LeBoeuf, M. Horning, J. Calambokidis, and D.A. Croll. 2000. Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* 288:133–136.
- Withers P.C. 1977. Measurement of $\dot{V}O_2$, $\dot{V}CO_2$, and evaporative water loss with a flow-through mask. *J Appl Physiol* 42:120–123.
- York A. 1994. The population dynamics of northern sea lions, 1975–1985. *Mar Mamm Sci* 10:38–51.
- Young R.A. 1976. Fat, energy, and mammalian survival. *Am Zool* 16:699–710.