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Energetic Costs and Thermoregulation in Northern Fur Seal (*Callorhinus ursinus*) Pups: The Importance of Behavioral Strategies for Thermal Balance in Furred Marine Mammals

Heather E. M. Liwanag*

Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95060

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ABSTRACT

Behavioral thermoregulation represents an important strategy for reducing energetic costs in thermally challenging environments, particularly among terrestrial vertebrates. Because of the cryptic lifestyle of aquatic species, the energetic benefits of such behaviors in marine endotherms have been much more difficult to demonstrate. In this study, I examined the importance of behavioral thermoregulation in the northern fur seal (*Callorhinus ursinus*) pup, a small-bodied endotherm that spends prolonged periods at sea. The thermal neutral zones of three weaned male northern fur seal pups (body mass range = 11.8–12.8 kg) were determined by measuring resting metabolic rate using open-flow respirometry at water temperatures ranging from 2.5° to 25.0°C. Metabolic rate averaged 10.03 ± 2.26 mL O₂ kg⁻¹ min⁻¹ for pups resting within their thermal neutral zone; lower critical temperature was $8.3^\circ \pm 2.5^\circ\text{C}$, approximately 8°C higher than the coldest sea surface temperatures encountered in northern Pacific waters. To determine whether behavioral strategies could mitigate this potential thermal limitation, I measured metabolic rate during grooming activities and the unique jughandling behavior of fur seals. Both sedentary grooming and active grooming resulted in significant increases in metabolic rate relative to rest ($P = 0.001$), and percent time spent grooming increased significantly at colder water temperatures ($P < 0.001$). Jughandling metabolic rate (12.71 ± 2.73 mL O₂ kg⁻¹ min⁻¹) was significantly greater than resting rates at water temperatures within the thermal neutral zone ($P < 0.05$) but less than resting metabolism at colder water temperatures. These data indicate that behavioral strategies may help to mitigate thermal challenges faced by northern fur seal pups while resting at sea.

Introduction

The high thermal conductivity and heat capacity of water compared with air make the ocean especially thermally challenging to endotherms (Dejours 1987). Numerous studies have shown elevated resting metabolic costs for aquatic and semiaquatic mammals in water (Fish 1979; Dawson and Fanning 1981; Costa and Kooyman 1982; Williams 1986; Williams et al. 2001). While raising metabolic rate is an effective mechanism by which to counteract heat loss, it represents an added energetic expense to the animal if employed over the long term.

In terrestrial environments, the importance of behavioral strategies for maintaining a favorable body temperature and reducing the energetic costs of thermoregulation has been demonstrated for a wide variety of endotherms. Thermoregulatory behaviors include postural changes, the selection of microhabitats, and huddling behavior (reviewed in Hafez 1964). These behaviors can impart a significant metabolic savings by reducing thermoregulatory costs and promoting survival in harsh environments (reviewed in Gilbert et al. 2009). One would expect in marine systems, where endotherms are faced with additional thermal challenges, that similar behavioral strategies may be used to offset the costs of thermoregulation. As such, behavioral modification may represent an important strategy for reducing thermoregulatory costs in the ocean. However, because of the cryptic habits of marine endotherms, the extent to which behavioral thermoregulation is utilized and its relation to overall energetic costs or savings are unknown for most species.

One known strategy for offsetting thermoregulatory costs is the recycling of metabolic heat produced by activity, termed thermal substitution. The concept of thermal substitution of heat produced by exercise is not new and has been demonstrated in several species of birds and rodents (reviewed in Lovvorn 2007). In marine systems, an increase in metabolic heat production associated with swimming exercise has been demonstrated for sea otters, pinnipeds, and cetaceans (Costa and Kooyman 1982, 1984; Williams 1999; Liwanag et al. 2009). The use of thermal substitution to mitigate thermal stress has also been demonstrated for other at-sea behaviors. Grooming behavior has been shown to be an important part of the thermal budget of the sea otter (Costa and Kooyman 1982; Yeates 2006), both because of its restoration of the insulating air layer in the fur and because of its potential for thermal substitution. The sea otter also uses the metabolic increase associated with newly ingested food (heat increment of feeding [HIF]) for thermoregulation (Costa and Kooyman 1984). It has been argued that

* Present address: University of California, San Diego, La Jolla, California 92093; e-mail: hliwanag@ucsd.edu.

the sea otter requires these behavioral strategies to maintain thermal balance because of its small body size and lack of a blubber layer (Costa and Kooyman 1982, 1984; Yeates et al. 2007).

Northern fur seals (*Callorhinus ursinus* L.), like sea otters, rely primarily on dense, waterproof fur for thermal insulation. The pups of this species wean at 4 mo of age at a body size approximately 85% that of an adult sea otter. On weaning, northern fur seal pups remain at sea on a pelagic migration lasting up to 21 mo (Gentry and Holt 1986; Baker 2007; Lea et al. 2009). Previous studies have shown that the combination of small body size and immature physiology makes fur seal pups and juveniles especially vulnerable to thermal stress in the water (Donohue et al. 2000; Rutishauser et al. 2004).

While at sea, fur seal species display an unusual posture known as the jughandle position, floating with both hind flippers and one foreflipper tucked and held above the water surface in an arc (Fig. 1). The purpose of this behavior is largely unknown, but popular hypotheses suggest opposing thermoregulatory consequences: the animals may remove the flippers from the water to avoid excessive heat loss to cold water, or they may position the flippers in the air to increase convective heat loss when warm (Bartholomew and Wilke 1956). Because the physiological consequences of jughandling behavior have yet to be measured, it has been difficult to distinguish the thermoregulatory significance of this behavior for fur seals.

In this study, I examined how behavioral strategies might help to mitigate thermal challenges encountered by northern fur seal pups during their first at-sea migration. This was accomplished by assessing the metabolic responses of weaned northern fur seal pups to different water temperatures. By determining the size of the thermal neutral zone (TNZ) and comparing the results to other marine mammals, I was able to quantify the relative thermal challenge experienced by post-

weaning fur seal pups. To evaluate the importance of behavioral strategies for thermoregulation, I measured the energetic consequences of resting, jughandling positions, and grooming behaviors on thermal metabolic responses in northern fur seals. Together these tests provided quantitative measurements of the energetic costs and benefits associated with thermoregulatory behaviors in a small-bodied marine endotherm.

Material and Methods

Animals

Three weaned male northern fur seal pups were used in this study (Table 1). The animals were rescued by the Marine Mammal Center in Sausalito, California, at approximately 6 mo of age (2 mo past the average weaning date for these animals), rehabilitated, and subsequently transferred to Long Marine Laboratory (University of California, Santa Cruz) for research. Fur seals were fully rehabilitated and determined by veterinary staff to be in releasable condition before experimentation. Experiments were conducted for 2 mo, during which the animals were approximately 7–9 mo of age. Fur seals were maintained in seawater pools and fed a daily diet of herring, capelin, and squid supplemented with vitamins. Water temperatures in the holding pools reflected ambient coastal water conditions and averaged 14.2°C (range: 10.7°–17.9°C) during the experimental period. Animal use was approved by the University of California Santa Cruz Chancellor's Animal Research Committee, approval Will05.01.

Protocol

For metabolic measurements, fur seals were conditioned over several weeks to enter a seawater pool (2.3 m × 2.3 m wide × 1.0 m deep) of known water temperature, over which



Figure 1. Northern fur seal pup in the jughandle position, with one foreflipper held between both hind flippers above the water. The other foreflipper is in the water and is assumed to help stabilize the animal in this position.

Table 1: Body mass, lower critical temperatures, and metabolic rates for northern fur seal pups

Animal	Body Mass (kg)	Lower Critical Temperature (°C)	Metabolic Rate (mL O ₂ kg ⁻¹ min ⁻¹)				
			Resting			Grooming	
			Postabsorptive	Postprandial ^{AB}	Jughandling ^A	Sedentary ^A	Active ^B
FS ₁	12.8 ± 2.4	6.6	7.75 ± 1.37	15.73 ± 0.73 ^a	13.09 ± 2.87	17.59 ± 1.21	17.83 ± 4.53
FS ₂	11.8 ± 2.2	7.2	9.15 ± 1.18	14.01 ± 0.61	10.93 ± 0.74	12.33 ± 1.39	21.03 ± 3.45
FS ₃	12.5 ± 2.9	11.1	11.37 ± 2.51	18.49 ± 2.53	NM	14.96 ± 3.47	22.95 ± 2.65
Mean	12.4 ± 0.5	8.3 ± 2.5	10.03 ± 2.26	16.25 ± 2.99	12.71 ± 2.73	15.15 ± 3.58	19.98 ± 4.32
N	3	3	22	4	18	11	29

Note. Values indicate means ± 1 SD. Resting metabolic rate was measured within the thermal neutral zone; other metabolic rates are for the indicated behaviors. Different letters indicate significant differences among metabolic rates. NM, not measured.

^aPostprandial metabolic rate was calculated during jughandling behavior for FS₁ and is not included in the mean for postprandial RMR.

a Plexiglas metabolic hood (approximately 114 cm wide × 175 cm long × 25 cm high) was mounted. The animals' movements were limited to an 84 × 86-cm basket (36 cm deep) comprised of PVC and netting, positioned directly beneath the metabolic hood. All three animals voluntarily and consistently entered the experimental apparatus for measurements. Water temperature was randomly varied between metabolic trials in approximately 2.5°C increments and ranged from 2.5° to 25.0°C. Temperature of the seawater was adjusted with ice or heated saltwater and was monitored throughout each trial. An experimental session consisted of a 60–120-min data acquisition period under the metabolic dome, with each animal tested only once per day. Behaviors were continuously monitored and recorded throughout each trial to synchronize metabolic rates with behavioral events.

Oxygen Consumption

Metabolic rate was determined from oxygen consumption measured by open-flow respirometry, using the protocols of Williams et al. (2002). Fur seals were fasted overnight (12 h) to ensure postabsorptive status at the time of measurement (Kleiber 1975), except for trials specifically assessing postprandial metabolism. Ambient air was drawn through the Plexiglas chamber at 60 L min⁻¹, with flow rates maintained and monitored continuously by a mass flow controller (Flowkit 500, Sable Systems, Las Vegas, NV). Samples of air from the exhaust port of the chamber were dried (Drierite; Hammond Drierite, Xenia, OH) and scrubbed of carbon dioxide (Sodasorb; Chemetron, St. Louis) before entering an oxygen analyzer (FC-1, Sable Systems). The percentage of oxygen in the expired air was monitored continuously and recorded once per second with a personal computer (Toshiba or Acer laptop) using Sable Systems software. Oxygen consumption ($\dot{V}O_2$) was then calculated using ExpeData software (Sable Systems International), modifying equation (4b) from Withers (1977) for this experimental setup. An assumed respiratory quotient of 0.77 was used in the calculations (Feldkamp 1987; Boyd et al. 1995; Arnould et al. 2001). Finally, all values were corrected to STPD. The entire system was calibrated daily with dry ambient air (20.94% O₂) and every 3–4 d with dry span gases (16.0% O₂)

and N₂ gas according to Fedak et al. (1981). In addition, the theoretical fraction of O₂ leaving the chamber was calculated according to Davis et al. (1985) and compared with measured values from the analyzer.

Determination of the TNZ

The TNZ is defined as the range of environmental temperatures in which an animal does not have to increase its metabolism above resting levels to maintain body temperature (Bartholomew 1977). Below the lower critical temperature (T_{LC}) or above the upper critical temperature (T_{UC}), an animal increases metabolism (and thus energetic cost) to offset heat loss or facilitate heat dissipation, respectively. The T_{LC} of each fur seal was determined from the break point for the relationship between mass-specific resting metabolic rate (RMR) and water temperature, from a segmented regression analysis minimizing the sum of the residual sum of squares (Sokal and Rohlf 1981; Nickerson et al. 1989). A computer program created for the determination of critical points (Yeager and Ultsch 1989) was used. The break point between the two lines of best fit defined the lower critical temperature. T_{LC} was determined separately for each individual (Table 1).

Behavioral Analyses

Behaviors during each metabolic trial were classified as resting, jughandling, grooming, or other (active) for the entire duration of the metabolic trial. Time spent performing each behavior was calculated as a percentage of total time for each metabolic trial. Behaviors such as shivering or sleeping, which were performed during another categorized behavior (i.e., resting or jughandling), were also noted.

Resting was defined as the animal floating quiescently with its flippers in the water while awake. Resting metabolism used for TNZ assessments was determined from fasting metabolic trials in which distinguishable resting bouts occurred. The lowest continuous oxygen consumption maintained for 5–10 min and corresponding to quiescent behavior was used in the analyses.

Because the ingestion and digestion of food increases met-

abolic rate (Webster 1983), two separate metabolic trials per fur seal were conducted immediately following 0.5–1.5-kg meals of herring, using the same experimental protocol as described above. Fur seals were fasted overnight (12 h) before the time of feeding. All feeding trials were conducted in water temperatures within the TNZ ($20.2^{\circ} \pm 0.3^{\circ}\text{C}$). The lowest oxygen consumption rate maintained for 10 min and corresponding to quiescent behavior was used to determine postprandial RMR.

Jughandling was defined as the animal floating with both hind flippers and one foreflipper held above the water surface in an arc (Fig. 1). Jughandling metabolism was analyzed for metabolic trials in which the animal consistently maintained the jughandle position for 30 min or more. Because the metabolic response of the animal changed during this behavior (Fig. 2), jughandling metabolic rate (JMR) was defined as the lowest consistent oxygen consumption maintained for 10 min, as determined by the analysis function “level” in the ExpeData program (Sable Systems International). JMR was calculated only for periods during which the animal was awake.

Grooming was defined as behavior directed toward maintenance or restoration of the air layer in the fur and included both rolling on the surface of the water and rubbing the fur with the flippers. Grooming was considered active if the animal was rolling or otherwise changing positions. Grooming was classified as sedentary if the animal was rubbing the fur with its flippers but otherwise maintaining a resting position on the water’s surface. Grooming metabolism was determined for continuous grooming bouts lasting 5–10 min. To examine whether grooming costs differed within and below the TNZ, the difference between grooming metabolism and RMR was calculated across water temperatures. Sedentary grooming and active

grooming were combined into a single category for activity budgets. Active periods not associated with grooming were not included in the metabolic analyses.

Statistical Analyses

All numerical values for oxygen consumption are presented as means \pm 1 SD. JMR was determined from the lowest-level oxygen consumption during this behavior and served as the reference for further jughandling analyses (Fig. 2). The added energetic cost of jughandling was determined by integrating under the oxygen consumption–time curve (ExpeData, Sable Systems International) and subtracting the baseline JMR for that trial. Thus, the resulting value represents the initial increased energetic cost (in mL O₂) associated with entering the jughandle position. This value was converted to joules, assuming $20.1 \times 10^3 \text{ J L}^{-1} \text{ O}_2$ (Schmidt-Nielsen 1997).

Statistical significance among levels of metabolism was determined by a linear mixed effects model, with individual seal as a random effects term, followed by a Bonferroni pairwise multiple comparison test (Systat Software, Chicago). Changes in activity budgets with water temperature were also determined by linear mixed effects models, with individual seal as a random effects term. Linear relationships between metabolic rates and water temperatures were calculated by least squares procedures (Zar 1974).

Results

Resting Metabolism and TNZ

Individual lower critical temperatures (T_{LC}) ranged from 6.6° to 11.1°C (Table 1). The mean T_{LC} for the fur seal pups was

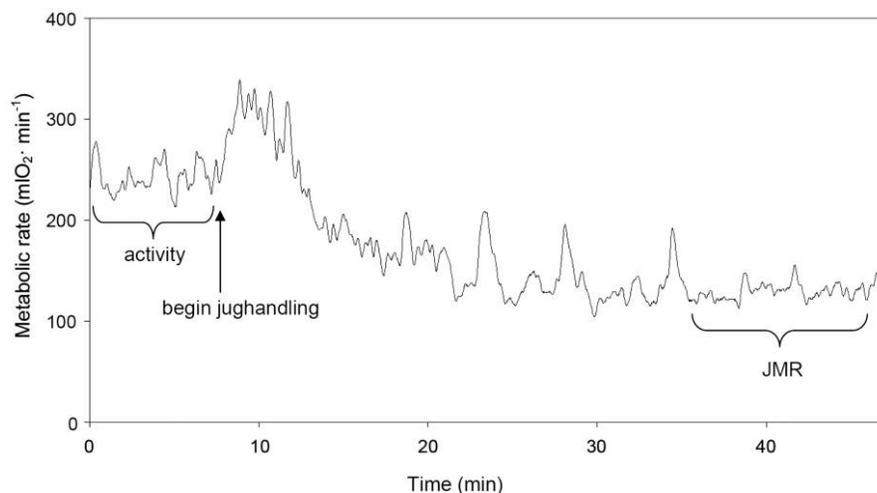


Figure 2. Representative metabolic trace for a northern fur seal exhibiting the jughandling posture, illustrating the characteristic changes in metabolic rate associated with this behavior. The initial portion of the trace corresponds to mild activity after the animal entered the metabolic chamber. Once the animal began jughandling, metabolism increased above the level associated with activity and then decreased in an approximately first-order recovery curve. The lowest steady state portion of the recovery curve (the section with the lowest standard deviation) was used to calculate jughandling metabolic rate (JMR), which then served as the baseline for integrating under the curve.

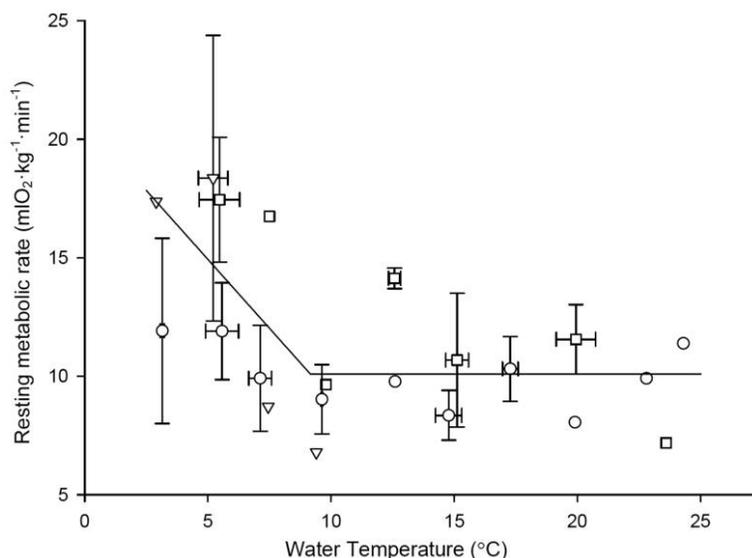


Figure 3. Resting metabolic rate in relation to water temperature for three northern fur seal pups. Each point represents the average of 1–3 independent trials for the same animal at similar temperatures, with error bars indicating ± 1 SD. Different symbols indicate different individuals. Lines represent the average results of segmented regression analysis. The temperature at the breakpoint of the two lines represents the lower critical temperature.

$8.3^\circ \pm 2.5^\circ\text{C}$ ($N = 3$ pups; Fig. 3; Table 1). This indicates a total TNZ of at least 16°C , since metabolic rate did not change significantly between 8.3° and 24.3°C ($F_{1,22} = 0.172$, $P = 0.682$).

The average metabolic rate of weaned northern fur seal pups resting in water within the TNZ was 10.03 ± 2.26 mL O_2 kg^{-1} min^{-1} ($N = 22$ trials; Table 1). Below the TNZ, resting metabolism increased as water temperature decreased, with individual fur seals exhibiting a 27%–168% increase in metabolism at the lowest experimental water temperatures (Fig. 3).

Metabolic rates after ingestion of food and during other behaviors were significantly different from RMR ($F_{4,73} = 29.427$, $P < 0.001$; random effects term [individual seal] was not significant). Postprandial RMR was measured for two of the three pups and averaged 16.25 ± 2.99 mL O_2 kg^{-1} min^{-1} ($N = 4$ trials). This value was significantly higher than RMR within the TNZ ($t = 3.593$, $P = 0.006$; Table 1; Fig. 4). The ingestion of fish did not elicit a defined peak in metabolic rate as previously reported for sea otters (Costa and Kooyman 1984) and pinnipeds (Markussen et al. 1994; Rosen and Trites 1997). Rather, feeding induced an increase in RMR relative to fasting levels within the TNZ, even at thermally neutral water temperatures. An average intake of 1.0 ± 0.6 kg of herring elicited an increase in resting energy output above baseline RMR levels that represented $9.7\% \pm 0.9\%$ of energy intake. Note that this value does not represent the full HIF but rather indicates the average resting metabolic increase elicited by prey ingestion in these animals.

Jughandling Metabolism

Two of the three fur seals exhibited jughandling behavior under the metabolic dome. For both animals, jughandling behavior elicited a characteristic metabolic response, in which metabolic rate first peaked and then decreased in an approximately first-order recovery curve (Fig. 2). On average, this metabolic elevation lasted approximately 30 min before reaching asymptote

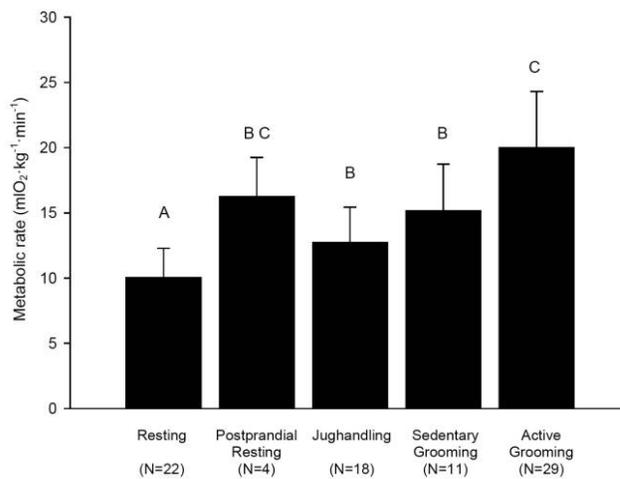


Figure 4. Metabolic rate according to behavior for northern fur seal pups. Heights of the bars and lines indicate means ± 1 SD. Different letters indicate statistically significant differences among means. Resting metabolism is for values within the thermal neutral zone.

and represented a 103% increase over the equilibrium jug-handling metabolism at the zenith. JMR was calculated from the asymptotic portion of the recovery curve (Fig. 2).

No break point could be defined for the relationship between JMR and water temperature, and JMR did not change significantly across the range of experimental water temperatures ($F_{1,13} = 0.712$, $P = 0.414$). One pup jughandled across nearly the entire range of experimental temperatures (FS_1 ; $T_{\text{water}} = 5.4^{\circ}\text{--}25.0^{\circ}\text{C}$), while one jughandled at warmer temperatures (FS_2 ; $T_{\text{water}} = 15.6^{\circ}\text{--}22.8^{\circ}\text{C}$). The average JMR across all water temperatures was 12.71 ± 2.73 mL O_2 kg^{-1} min^{-1} ($N = 18$ trials) and was significantly higher than RMR within the TNZ ($t = 2.989$, $P = 0.038$; Table 1; Fig. 4). This result is consistent with a previous report of elevated JMR relative to RMR in preweaned northern fur seal pups (Donohue et al. 2000).

Integration under the jughandling curves revealed that the animals expended 42.5 ± 33.8 kJ of additional energy above the equilibrium JMR during an average of 48.7 ± 14.8 min in the jughandle position. Once the metabolism reached equilibrium, jughandling still represented a 39% increase over RMR on average.

Postprandial JMR was measured for one pup (FS_1) and averaged 16.73 ± 0.73 mL O_2 kg^{-1} min^{-1} ($N = 2$ trials). Postprandial JMR was not significantly different from fasting JMR for this animal ($t = 2.14$, $P = 0.23$; Table 1).

Grooming Metabolism

Metabolism during sedentary grooming, 15.15 ± 3.58 mL O_2 kg^{-1} min^{-1} ($N = 11$ trials), was significantly greater than RMR within the TNZ ($t = 4.152$, $P = 0.001$; Table 1; Fig. 4) and represented an increase of 1.3–2.3 times RMR for individual fur seals. Sedentary grooming metabolism did not change significantly with water temperature ($F_{1,7} = 5.128$, $P = 0.058$; $T_{\text{water}} = 3.1^{\circ}\text{--}17.5^{\circ}\text{C}$). In comparison, metabolism during active grooming, 19.98 ± 4.32 mL O_2 kg^{-1} min^{-1} ($N = 29$ trials), was significantly greater than sedentary grooming metabolism ($t = 4.371$, $P < 0.001$; Table 1; Fig. 4). As found for sedentary grooming, active grooming metabolism did not change significantly with water temperature ($F_{1,22} = 1.912$, $P = 0.181$; $T_{\text{water}} = 2.9^{\circ}\text{--}24.3^{\circ}\text{C}$). The difference between grooming metabolism and RMR was significantly lower below the T_{LC} compared with the difference within the TNZ ($F_{1,22} = 16.711$, $P < 0.001$).

Effects of Water Temperature on Behavior

For all three fur seals, the percent time resting did not change significantly with temperature ($F_{1,52} = 0.924$, $P = 0.341$). Interestingly, percent time jughandling increased significantly with temperature ($F_{1,52} = 14.449$, $P < 0.001$), though jughandling behavior was rarely observed during the metabolic trials in one of the animals (FS_3). All three fur seals exhibited a significant increase in percent time grooming as temperature decreased ($F_{1,52} = 40.725$, $P < 0.001$; Fig. 5); this was the primary behavioral pattern that was consistently observed among

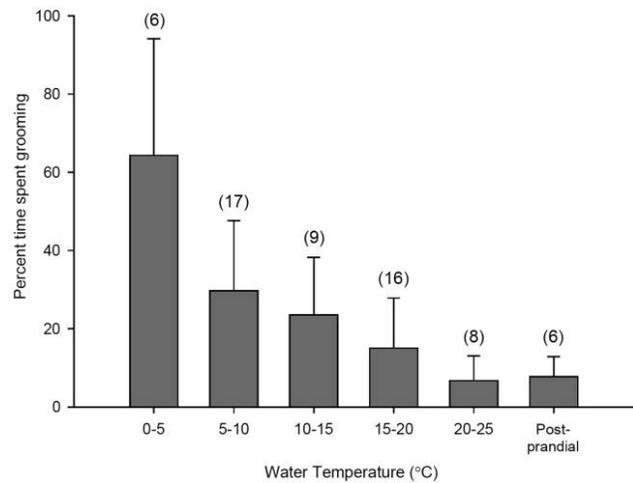


Figure 5. Percent time spent grooming in relation to water temperature for three northern fur seal pups. Postprandial indicates time spent grooming after the ingestion of food in warm water ($20.2^{\circ} \pm 0.3^{\circ}\text{C}$). Numbers in parentheses indicate the number of independent trials included in each temperature bin.

all three individuals. In contrast, the percent time spent performing other activities did not change significantly across temperatures ($F_{1,15} = 1.843$, $P = 0.180$). Shivering occurred during either resting or jughandling behavior, across the range of experimental temperatures, and did not change significantly with temperature for any of the fur seals ($F_{1,52} = 0.195$, $P = 0.661$).

Discussion

Thermal Capabilities of Northern Fur Seal Pups

During the transition to independence, young pinnipeds will eventually access the same range of oceanic foraging grounds as adult conspecifics. Several physiological challenges must be overcome for the young animals to successfully accomplish this transition. First, young pinnipeds do not exhibit the same physiological and behavioral diving capacities as adults. Limitations include higher mass-specific metabolic rates (Fowler et al. 2006; Richmond et al. 2006), lower oxygen stores (Noren et al. 2001; Burns et al. 2004), and inexperience constraining dive behavior (Le Boeuf et al. 1996; Merrick and Loughlin 1997). Another factor comprises thermal energetic costs associated with immersion, which are greater in smaller, immature animals compared with adults. As a result of these factors, the foraging range of pups may be limited, both geographically and within the water column, at a critical point in their life history.

Thermal limitations in water have been reported previously for young otariids (Table 2). For example, the T_{LC} of juvenile California sea lions ($>12^{\circ}\text{C}$) is several degrees higher than the range of water temperatures typically encountered, indicating a thermal challenge for the young of this species (Liwanağ et al. 2009). Likewise, both pup and juvenile Antarctic fur seals demonstrate thermal energetic costs that potentially limit the

Table 2: Lower critical temperatures (T_{LC}) for sea otters and pinnipeds resting in water

Species and Age Class	Average Body Mass (kg)	T_{LC} (°C)	Water Temperatures Encountered (°C)	Source
Sea otter, <i>Enhydra lutris</i> :				
Adult	17.3	20	0–20	Costa and Kooyman 1982
Northern fur seal, <i>Callorhinus ursinus</i> :				
Pup (preweaning, premolt)	8.3	>10	0–20	Donohue et al. 2000
Pup (preweaning, postmolt)	14.8	~10	0–20	Donohue et al. 2000
Pup (postweaning)	12.4	8.3	0–20	This study
Antarctic fur seal, <i>Arctocephalus gazella</i> :				
Pup	13.6	14.4	0–5	Rutishauser et al. 2004
Juvenile	17.3	14.4	0–10	Rutishauser et al. 2004
California sea lion, <i>Zalophus californianus</i> :				
Juvenile	32.6	>12	10–30	Liwanag et al. 2009
Adult	94.7	6.4	10–30	Liwanag et al. 2009
Harbor seal, <i>Phoca vitulina concolor</i> :				
Juvenile:				
Summer	27.4	20	15–30	Hart and Irving 1959
Winter	33.7	13	8–23	Hart and Irving 1959
Harp seal, <i>Phoca groenlandica</i> :				
Juvenile	38.6	<0	–2–5	Irving and Hart 1957
Adult	140.7	<0	–2–10	Gallivan and Ronald 1979

Note. Values are compared with the range of water temperatures typically encountered by each species in the wild. Body mass and T_{LC} values are estimated from the sources indicated. Water temperatures are the routine sea surface temperatures encountered by each species and age class (NASA Moderate Resolution Imaging Spectroradiometer database).

range of foraging and may prevent these age classes from utilizing adult foraging grounds (Rutishauser et al. 2004).

I have also found that thermal limitations may occur in weaned northern fur seal pups (Table 2). While the molting of the natal pelage helps to increase thermal insulation of northern fur seal pups immediately before weaning, the preweaned pups still show elevated metabolic rates at water temperatures regularly encountered in the wild, even in coastal regions close to the rookery (Donohue et al. 2000). This study shows that the thermal capabilities of weaned northern fur seal pups have changed relative to preweaned, postmolt pups. RMR within the TNZ (Table 1) was lower than what Donohue et al. (2000) reported for postmolt pups before weaning and is consistent with the expected reduction in mass-specific metabolism with age (Kleiber 1975). This effect appears to be due to age rather than body size per se, since the animals in this study were smaller than the pups in the study by Donohue et al. (2000; Table 2), though within the range of weaning masses for this species (Boltnev et al. 1998). In addition, the T_{LC} of $8.3^\circ \pm 2.5^\circ\text{C}$ measured here for weaned pups is lower than estimated for pups before weaning (Table 2; Donohue et al. 2000). The combination of a lower RMR and a lower T_{LC} indicates that these animals are able to tolerate a wider range of temperatures without expending extra metabolic energy, suggesting an improvement in thermal capabilities associated with the transition to independence.

The comparatively low T_{LC} of northern fur seal pups indicates

a remarkable tolerance for cold water temperatures despite the small body size of these young animals, particularly in comparison to other otariid species (Table 2). The T_{LC} of weaned northern fur seal pups is also considerably lower than that of the sea otter, a similarly sized marine mammal that also relies on fur for its primary insulation. Despite a denser pelage (Williams et al. 1992), adult female sea otters exhibit a T_{LC} approaching 20°C (Costa and Kooyman 1984), more than 10°C higher than measured here for northern fur seal pups. Overall, the relatively low RMR and T_{LC} measured in this study signify that northern fur seal pups exhibit exceptional thermal capabilities for their young age and small body size.

Developmental improvements notwithstanding, the T_{LC} of weaned northern fur seal pups remains higher than the routine sea surface temperatures found in the northern Pacific Ocean (Table 2; Fig. 6), where newly weaned pups spend up to 21 mo diving in pelagic waters (Gentry and Holt 1986; Baker 2007; Lea et al. 2009). Just after weaning, sea surface temperatures in the north Pacific range from 0° to around 20°C . However, during the colder winter months, temperatures can fall below 1°C in the northern parts of the foraging grounds (Fig. 6). This has profound implications for rest periods at sea. While heat generated by activity may offset excessive heat loss when swimming, resting periods may easily result in a thermal deficit. For example, the fur seals in this study demonstrated increases in resting metabolism between 27% and 168% above baseline values at colder water temperatures (Fig. 3), suggesting that rest

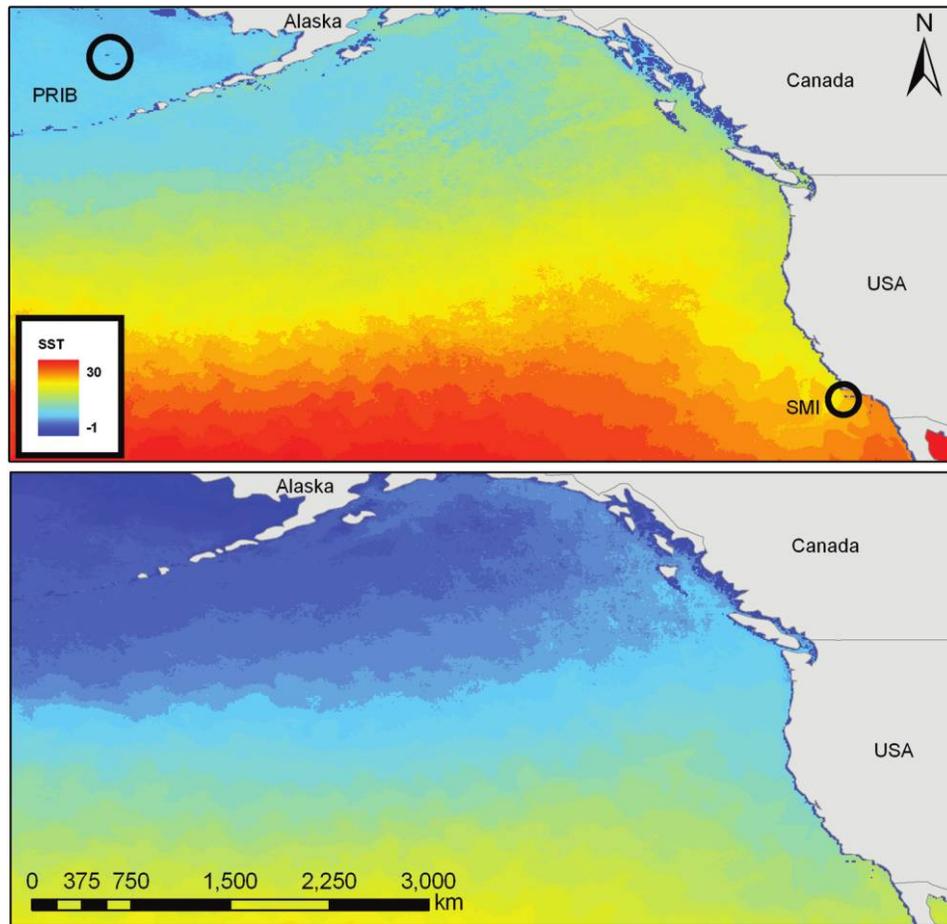


Figure 6. Sea surface temperatures (SST) in the northern Pacific during November 2006 (*top*) and January 2007 (*bottom*). Northern fur seal pups wean in November from rookeries in the Pribilof Islands (*PRIB*) and San Miguel Island (*SMI*). The animals then spend between 9 and 21 mo foraging in the northern Pacific basin. Sea surface temperatures were obtained from the NASA Advanced Very-High-Resolution Radiometer database (BloomWatch 360).

periods are likely to be energetically costly to these animals even within their natural water temperature range.

These high thermal energetic costs for northern fur seal pups may be associated with the use of fur as the primary form of insulation in water, since a similar thermal liability during rest is observed for many small-bodied, furred marine mammal species (Fig. 7). Here I define thermal liability as the difference between the animal's T_{LC} in water and the lowest sea surface temperature routinely encountered by the species and age class of interest. Comparing thermal liabilities among species reveals that the use of blubber as the primary form of insulation, along with an associated increase in body size, reduces the level of liability in young pinnipeds and eliminates it for adult sea lions and phocids (Fig. 7). Thus, while sea otters and immature fur seals exhibit thermal liabilities of at least 8°C while resting at sea, immature harbor seals and California sea lions, which rely on blubber for their insulation, have thermal liabilities of only 5°C. Young harp seals, an ice-dwelling species that relies on a thick blubber layer for insulation, have a T_{LC} below 0°C and

thus no thermal liability even when living above the Arctic circle. Interestingly, adult sea lions and harp seals maintain negative thermal liabilities; in other words, the T_{LC} is lower than the coldest sea surface temperatures encountered, thereby affording the animals the benefit of low thermal energetic costs during rest periods. Overall, these comparisons suggest a thermal advantage for larger-bodied marine mammals using blubber for insulation compared with small-bodied marine mammals using fur.

The Effects of Behavioral Strategies on Thermal Responses in Northern Fur Seal Pups

The use of behavioral strategies to mitigate thermal limitations has been demonstrated for terrestrial species (Hafez 1964; Hart 1971; Whittow 1971) and for pinniped species on haulouts (Irving et al. 1962; Peterson et al. 1968; Gentry 1972; Odell 1974). However, far less is known about the behavioral strategies employed by marine mammals at sea. I have previously

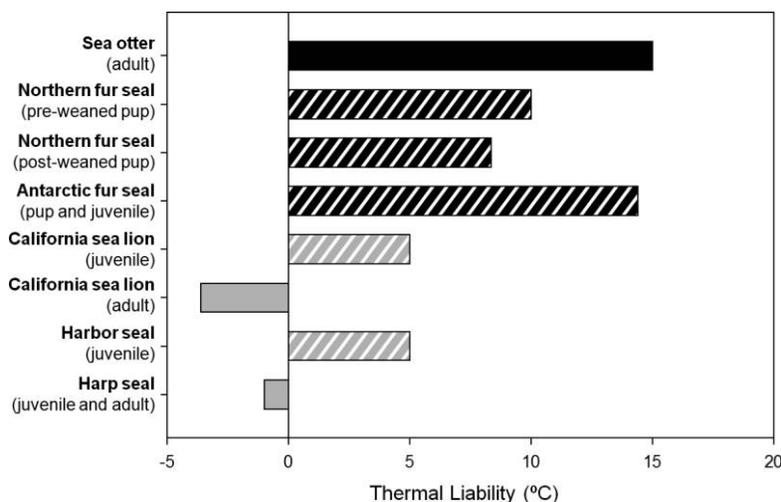


Figure 7. Comparison of the thermal liability of sea otter and pinniped species in water. Thermal liability is calculated as the difference between the lower critical temperature (T_{LC}) in water and the lowest sea surface temperature routinely encountered. Black bars indicate species with waterproof fur as the primary insulating layer, and gray bars indicate species with blubber as the primary insulating layer. Plain bars include adult animals, and hatched bars indicate pups or juveniles.

reported that young otariids utilize the recycling of heat generated by swimming activity to offset thermal limitations during swimming (Liwanag et al. 2009). However, a question remains regarding thermal costs during periods of rest. Coastal sea lions may haul out on shore during these periods (Reeves et al. 2002). This is not possible for young northern fur seals, which are pelagic and must rest at sea. Because young fur seals cannot use swimming activity to offset excessive heat loss when resting, they utilize several other behavioral strategies.

Jughandling Behavior. Thermoregulatory explanations for jughandling behavior propose that removal of the flippers from the water may decrease heat loss in cold water or facilitate heat dissipation in warm water (Bartholomew and Wilke 1956). The occurrence of jughandling behavior across the full range of experimental water temperatures in this study suggests that these hypotheses may not be mutually exclusive. The large, poorly insulated flippers of fur seals serve as important thermal windows—areas through which the animals can easily dissipate heat (Bryden and Molyneux 1978). Many species of marine mammal use poorly insulated areas as thermal windows, including sea otters (Tarasoff 1972, 1974), otariids (Ohata and Miller 1977), phocids (Molyneux and Bryden 1978; Rommel et al. 1995), and cetaceans (Hampton and Whittow 1976; Meagher et al. 2000). Peripheral sites such as the flippers remain the primary option for heat transfer in furred species such as fur seals (Bryden and Molyneux 1978; Schmidt-Nielsen 1997).

Because the flippers are highly vascularized and contain countercurrent arrangements of blood vessels (Tarasoff and Fisher 1970; Bryden and Molyneux 1978), fur seals have control over the extent to which heat is moved across the flippers. In view of this, the thermoregulatory consequences of jughandling may depend largely on blood flow. Interestingly, there appears

to be a metabolic cost associated with the jughandle position itself, such that the metabolism increases once the animal begins jughandling, reaches a peak, and then declines to a steady state JMR (Fig. 2). This initial cost to the jughandle position may be associated with changes in perfusion. It is quite possible that jughandling enables perfusion of the flippers in both cold and warm water. With the flippers immersed in cold water, the thermal windows would be “shut” and blood flow to the flippers reduced, but placing the flippers in air would enable perfusion of the flippers with reduced heat loss to the surroundings. In warm water, increased blood flow to the flippers during jughandling would enable heat dissipation to the air. In both cases, perfusion of the flippers may be associated with a temporary increase in metabolic rate, as the body adjusts to the shifts in blood flow. Thus, the combination of physiological control of blood flow with the behavioral posture of jughandling may allow fur seals to exhibit a dynamic response to a range of environmental temperatures.

It is possible that jughandling behavior affords an extension of the effective TNZ for northern fur seal pups. Equilibrium JMR is significantly higher than RMR and thus represents elevated costs within the TNZ (Fig. 4). However, for the fur seal (FS₁) that exhibited jughandling behavior in cold water, JMR was significantly lower than RMR at water temperatures below the T_{LC} ($t = 2.64$, $P = 0.018$). These findings indicate a potential energetic benefit associated with jughandling behavior at low water temperatures, in this case a savings of 45 J min^{-1} at equilibrium. Because JMR typically took at least 30 min to reach equilibrium, any energetic savings that might be associated with this behavior would require it to be used as a long-term strategy, conferring thermal benefits over time that may counterbalance the initial costs.

The added cost of jughandling within the TNZ indicates that

there may be other explanations for this behavior as well. Because fur seals are known to sleep in the jughandle position (Donohue et al. 2000), it may be that jughandling provides a stable resting position for sleeping at sea. Perhaps jughandling enables fur seals to cast a silhouette that is less conspicuous to predators from below. While these are possible benefits for this behavior within the TNZ, they do not explain why the behavior requires added metabolic energy above RMR, even at equilibrium. This added energy expenditure suggests that jughandling does affect the animal's physiology in some way, and changes in blood flow to the flippers could be one explanation.

Grooming Behavior. Grooming behavior restores the air layer to the fur and is therefore necessary to ensure insulation in furred endotherms living in aquatic environments. As reported for sea otters (Costa and Kooyman 1982; Yeates et al. 2007), I found a significant increase in metabolic rate associated with grooming behavior for northern fur seal pups (Fig. 4). In addition, grooming behavior represented a greater proportion of fur seals' activity budgets at colder water temperatures (Fig. 5). Below the T_{LC} , grooming costs represented a significantly smaller increase in metabolism over RMR, providing evidence for thermal substitution. Similar to the use of thermal substitution observed in exercising birds and mammals (Williams 1983; Lovvorn 2007; Liwanag et al. 2009), fur seals can use the increased heat production associated with grooming to mitigate thermal costs at sea. Thus, grooming behavior in furred marine mammals could have the dual purpose of restoring the effectiveness of the insulation and serving as a strategy to counteract heat loss in cold water with increased heat production.

The Effects of Ingested Prey Items on Thermal Responses in Northern Fur Seal Pups

Increases in metabolism associated with the ingestion and digestion of food have been demonstrated for a variety of vertebrates, including fish (Beamish and MacMahon 1988), reptiles (Andrade et al. 1997), birds (Hawkins et al. 1997; Schieltz and Murphy 1997), and mammals (Markussen et al. 1994; Rosen and Trites 1997; Nespolo et al. 2003). The importance of this HIF for thermal substitution, though not universal, has been shown both for birds (Chappell et al. 1997; Kaseloo and Lovvorn 2003; Bech and Præsteng 2004) and for mammals (Costa and Kooyman 1984; Jensen et al. 1999). For sea otters in particular, HIF is an important part of the thermal budget, enabling increased rest periods in water temperatures outside the TNZ (Costa and Kooyman 1984; Yeates et al. 2007). Although postprandial RMR was not measured outside the TNZ for the fur seals in this study, an increase in RMR associated with food ingestion was observed within the TNZ (Fig. 4), demonstrating that increased heat production associated with digestive processes does occur in this species. As observed for grooming, this increased heat production could act as an important source of thermal substitution for northern fur seal pups in colder water temperatures.

Postprandial RMR for the fur seals in this study was 58%

higher than postabsorptive RMR, representing 9.7% of ingested energy. These values are consistent with the magnitudes reported for other marine mammals, including the sea otter (Costa and Kooyman 1984), harbor seal (Markussen et al. 1994), and Steller sea lion (Rosen and Trites 1997). Interestingly, postprandial jughandling metabolism was not significantly different from postabsorptive jughandling metabolism for one fur seal (FS₁; Table 1), which may be due to dissipation of excess heat during jughandling at warmer water temperatures.

Conclusions

In summary, the metabolic responses of weaned northern fur seal pups indicate an impressive tolerance to cold water but still suggest the potential for thermal costs while resting at sea. As found with other furred marine species, the use of thermal substitution from a variety of sources can help to mitigate these costs in young fur seals during their first migration. This study found that grooming behavior in particular provides significant thermal benefits, especially at colder water temperatures. Jughandling behavior may help fur seals retain or dissipate heat in cold or warm water, respectively. Overall, behavioral thermoregulation represents a potentially important mechanism for ensuring thermal stability in small-bodied marine mammals that rely primarily on fur for insulation.

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