Marine Mammal Science

MARINE MAMMAL SCIENCE, 30(3): 994–1013 (July 2014)

DOI: 10.1111/mms.12103

Broad thermal capacity facilitates the primarily pelagic existence of northern fur seals (*Callorhinus ursinus*)

ALEX J. M. DALTON,[1] DAVID A. S. ROSEN and ANDREW W. TRITES, Department of Zoology and Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, 2202 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada.

ABSTRACT

Thermoregulatory capacity may constrain the distribution of marine mammals despite having anatomical and physiological adaptations to compensate for the thermal challenges of an aquatic lifestyle. We tested whether subadult female northern fur seals (*Callorhinus ursinus*) experience increased thermoregulatory costs in water temperatures potentially encountered during their annual migration in the Bering Sea and North Pacific Ocean. Metabolic rates were measured seasonally in 6 captive female northern fur seals (2.75–3.5 yr old) in ambient air and controlled water temperatures of 2°C, 10°C, and 18°C. Rates of oxygen consumption in ambient air (1°C–18°C) were not related to environmental temperature except below 2.5°C (winter only). However, metabolism was significantly higher during the fall seasonal trials (September–October) compared to other times of year, perhaps due to the costs of molting. The fur seals appeared thermally neutral in all seasons for all water temperatures tested (2°C–18°C) except during the summer when metabolic rates were higher in the 2°C water. Comparing this broad thermal neutral zone to the average sea surface temperatures potentially encountered during annual migrations indicates wild fur seals can likely exploit a large geographic area without added thermal metabolic costs.

Key words: northern fur seal, *Callorhinus ursinus*, thermal neutral zone, thermoregulation, metabolism.

Physiological and anatomical modifications are required to live in an aquatic environment and offset the thermal properties of water, which conducts heat away from the body 24 times faster than air of the same temperature (Dejours 1987). Specialized insulation is one common adaptation among marine mammals and other endotherms to reduce heat loss to the environment (Scholander *et al*. 1950, Williams and Worthy 2002). In many species of marine mammals, insulation from the aquatic environment is accomplished *via* a thick subcutaneous lipid (blubber) layer (Scholander *et al.* 1950, Strandberg *et al.* 2008, Liwanag *et al.* 2012*b*). However, some aquatic and semiaquatic mammals, such as beavers, otters, and fur seals, have thin subcutaneous lipid layers, and rely instead upon a dense pelage and its associated structures for insulation during immersion (Irving *et al.* 1962, Williams *et al.* 1992, Liwanag *et al.* 2012*a*).

---

[1] Corresponding author (e-mail: a.dalton@fisheries.ubc.ca).

Unfortunately, even a dense pelage may not provide sufficient insulation against the cold-water conditions that furred mammals are likely to encounter. Lower critical temperatures (LCT) in water, the temperature below which homeotherms must expend additional energy to maintain their body temperature, are reported to be 20°C for sea otters (*Enhydra lutris;* Costa and Kooyman 1982) and 14.4°C for juvenile (pup and yearling) Antarctic fur seals (*Arctocephalus gazella*; Rutishauser *et al.* 2004). The fact that these lower critical temperatures are well above the usual water temperatures of their habitats implies that increased metabolic rates are required to maintain the core body temperatures of these and potentially other marine mammals that rely upon dense pelages for insulation (Costa and Kooyman 1982, Williams and Worthy 2002, Rutishauser *et al.* 2004).

Elevated resting metabolic rates, compared to similar sized terrestrial mammals, have been measured in many species of marine mammals, including several species of pinnipeds (Irving and Hart 1957, Costa and Kooyman 1982, Kasting *et al.* 1989, Hurley and Costa 2001, Williams *et al.* 2001, Boyd 2002). An increased metabolic rate is an effective short-term solution for maintaining core body temperatures and is a normal physiological response to environmental temperatures that are outside of the thermal neutral zone (TNZ) of an individual (Irving and Hart 1957, Gordon *et al.* 1972, Williams and Worthy 2002, Liwanag 2010). However, an increased metabolic rate represents a substantial added energetic expense if used as a long-term adaptation (Williams and Worthy 2002, Liwanag *et al.* 2009). As a result, the geographic range of most endotherms is likely constrained in part by thermal considerations (Angilletta 2009).

The northern fur seal (*Callorhinus ursinus*) is a species of pinniped that is assumed to depend primarily on its pelage for insulation, based on the thinness of its fat layer (Blix *et al.* 1979) and other morphological evidence (Liwanag *et al.* 2012*a*, *b*). However, past studies have failed to reach a consensus on the thermal capabilities of young northern fur seals—although the lower critical water temperature is commonly estimated to be between 4°C and 10°C (Donohue *et al.* 2000; Liwanag 2010; Rosen and Trites, in press), one study placed the LCT at >18°C (Miller 1978). This last estimate falls within the range of lower critical water temperatures of 15°C–20°C reported for similar sized (nonpup) aquatic and semiaquatic mammals with dense pelages (Dawson and Fanning 1981, Costa and Kooyman 1982, Williams 1986, Rutishauser *et al.* 2004).

The thermal neutral zone of juvenile northern fur seals is of more than simply an academic interest. Environmental water temperatures below the LCT will cause northern fur seals to increase their metabolic rates to generate replacement body heat. These higher energy demands would have to be offset by increased food intake, and would potentially exclude the fur seals from exploiting habitats where satisfying the additional energetic costs of thermal regulation may be too high.

There are only three major breeding colonies of northern fur seal in North America (DeLong 1982, Loughlin and Miller 1989, Gentry 1998, COSEWIC 2010, Testa 2011). Each fall, individuals from two of these colonies—the Pribilof and Bogoslof Islands in Alaska—migrate from the Bering Sea to the North Pacific Ocean, travelling as far south as California (Kenyon and Wilke 1953, Bigg 1990, Gentry 1998, Ream *et al.* 2005). Adult females and juveniles of both sexes make a more extensive migration than adult males, to either the transitional region of the central North Pacific Ocean or across the North Pacific Ocean to the continental margins of North America (Kenyon and Wilke 1953, Bigg 1990, Gentry 1998, Ream *et al.* 2005). In contrast to the fur seals breeding in the Bering Sea, females from the third colony

(San Miguel Island, California) have a less extensive pelagic migration (male distribution and migration remains unknown), remaining near the continental margins of North America throughout most of the year (primarily California), and shifting their distribution northward and offshore during the winter (Melin *et al.* 2012).

The lengthy migration of the northern fur seal (late fall to early summer) makes it difficult to evaluate the thermal capacity of this species in direct relation to environmental conditions (Kenyon and Wilke 1953, Bigg 1990, Gentry 1998, Ream *et al.* 2005). The extent to which their migration patterns are constrained by thermal capabilities is unknown, as is the degree to which environmental temperatures might affect thermoregulatory costs and subsequent prey requirements in certain foraging areas.

We measured the thermal costs of aquatic exposure in northern fur seals to quantify the potential energetic expenses associated with their pelagic existence and to investigate whether the thermal capabilities of this species might limit their seasonal distribution. Specifically, we measured the metabolic rates of captive northern fur seals (juvenile females) in water temperatures between 2°C and 18°C and compared them to metabolic rates when resting in dry ambient air conditions. We also investigated the thermoregulatory abilities of the individuals over the course of the year to explore potential seasonal changes. These thermoregulatory abilities were then compared to the documented average sea surface temperatures along the generalized migration routes of female and juvenile northern fur seals. We examined whether their generalized migration route appeared constrained by these thermal costs, or whether these routes took them outside of their thermal neutral zone. This allowed us to identify potentially critical times of year when elevated metabolic rates due to thermoregulatory demands and increased food requirements might be expected.

METHODS

Animals

Six female northern fur seals (ages 2.75–3.50 yr) participated in this study from March 2011 to January 2012 (Table 1). The animals came from a rookery on St. Paul Island, Alaska (one of the Pribilof Islands) in October 2008, following weaning at approximately 4 mo of age. The individuals were transported to the University of British Columbia's Marine Mammal Energetics and Nutrition Laboratory, located at the Vancouver Aquarium, British Columbia, Canada. They were raised in captivity and trained with positive reinforcement to be familiar with all necessary research protocols and equipment. The fur seals normally consumed a daily diet of herring and squid, supplemented with vitamins, and were housed in seawater pools with water temperatures that reflected the local ocean conditions (7°C–16°C).

Protocol and Timing

Four seasonal sets of metabolic measurement trials were conducted during the study period: March/April 2011 ("Spring"; individuals 2.75 yr old), June/July ("Summer"; age 3 yr), September/October ("Fall"; age 3.25 yr), and December 2011/January 2012 ("Winter"; age 3.5 yr), with each set of trials taking approximately 4–6 wk to complete. Within each set of trials, the metabolic rate of each individual (see below) was tested both in ambient air conditions as well as at three different water temperatures: 2°C, 10°C, and 18°C (±0.5°C).

Table 1. Body mass (kg) and mass-specific rate of oxygen consumption resting in dry ambient air conditions ($\dot{V}O_{2air}$; mL O_2 kg^{-1} min^{-1}) during four seasonal trials (spring, summer, fall, and winter) for each of the six female northern fur seals from March 2011 to January 2012. Mean ± SD are presented for all six animals as well as for the truncated data set resulting from the removal of individual ME08 that did not behaviorally meet resting conditions.

	Spring		Summer		Fall		Winter	
Animal	Body mass	$\dot{V}O_{2air}$	Body mass	$\dot{V}O_{2air}$	Body mass	$\dot{V}O_{2air}$	Body mass	$\dot{V}O_{2air}$
AN08	19.8 ± 0.6	13.4 ± 2.0	21.2 ± 0.9	11.4 ± 0.1	22.2 ± 0.5	18.1 ± 4.5	21.2 ± 0.3	14.1 ± 8.3
AY08	14.2 ± 0.08	14.6 ± 1.0	17.0 ± 0.9	11.9 ± 1.3	18.4 ± 0.09	20.3 ± 2.6	17.7 ± 0.3	13.3 ± 4.5
KY08	15.3 ± 0.05	11.3 ± 0.4	17.6 ± 0.8	14.0 ± 2.0	19.5 ± 0.1	18.1 ± 4.6	15.6 ± 0.2	13.3 ± 2.0
ME08	15.6 ± 0.2	25.2 ± 2.8	17.1 ± 0.4	23.0 ± 5.7	19.8 ± 0.3	36.5 ± 2.5	19.3 ± 0.1	29.4 ± 10.1
TI08	18.9 ± 0.2	14.6 ± 1.0	22.6 ± 0.6	12.3 ± 2.4	26.6 ± 0.8	17.8 ± 2.2	25.1 ± 0.1	8.8 ± 3.1
TU08	15.2 ± 0.1	14.1 ± 1.7	18.6 ± 0.8	21.9 ± 3.7	21.4 ± 0.3	22.2 ± 2.5	20.3 ± 0.4	25.0 ± 5.3
Mean (all animals)	16.5 ± 2.3	15.2 ± 5.1	19.0 ± 2.3	15.7 ± 5.3	21.4 ± 2.9	22.1 ± 7.2	20.5 ± 2.5	17.3 ± 8.0
Mean (ME08 omitted)	16.7 ± 2.5	13.1 ± 1.4	19.4 ± 2.4	14.3 ± 4.3	21.7 ± 3.1	19.3 ± 1.9	20.8 ± 2.7	14.9 ± 6.0

On three separate occasions within each season (once for each water temperature treatment), each fur seal voluntarily entered a specially designed 340 L metabolic chamber (dimensions: 0.92 m × 0.61 m × 0.61 m) under trainer control. The individuals were trained to remain calm, with minimal activity, within the chamber. Rates of oxygen consumption and carbon dioxide production of the fur seal were continuously measured in the metabolic chamber for 20 min in dry ambient air conditions. Immediately following the dry ambient air measures, the chamber was filled two-thirds full (sufficient to cover the animal's entire torso, but prevent swimming) with water at one of the three different treatment temperatures (2°C, 10°C, or 18°C). It took approximately 5 min to fill the chamber and mechanical fail-safes prevented the water level from rising above the set point. Once immersed, rates of oxygen consumption and carbon dioxide production were again continuously measured for an additional 30 min (consistent with Donohue *et al.* 2000; and supported by the time required for heat flux density measurements through the skin of newborn northern fur seals to reach steady state, Blix *et al.* 1979), with water continuously being pumped through the chamber from a large temperature-controlled reservoir.

Trials were conducted in the morning and individuals were tested only once daily. Individuals were fasted overnight (>16 h) to ensure a postabsorptive state had been reached. The order of water temperature treatments tested was consistent (10°C, 2°C, and 18°C) within each trial block. Animal behavior, air temperature and water temperature (when appropriate) were recorded every 5 min throughout each trial.

Metabolic Rate

Open flow respirometry was used to measure rates of oxygen consumption and carbon dioxide production to determine metabolic rates. Measurements were made using one of two systems. First, ambient air was drawn through the metabolic chamber at 125 L/min *via* either the Sable Systems Model 500H Mass Flow Controller (Sable Systems, Las Vegas, NV) or the Sable Systems Field Metabolic Pump, both of which constantly corrected the flow rate to standard temperature and pressure. Next, subsamples of air from the excurrent airstream were dried through a canister of anhydrous $CaSO_4$ (Drierite; Hammond Drierite, Xenia, OH), before the O_2 and CO_2 concentration were analyzed by the Sable Systems FC-1B and CA-1B analyzers, respectively, or using the Sable Systems Field Metabolic System (P-Series). The resultant O_2 and CO_2 concentrations in the excurrent air were continuously monitored and recorded to a portable computer using Sable Systems' Expedata software.

The entire gas analysis system was calibrated with dry ambient air prior to and following each trial, such that changes in gas concentrations were determined against baseline (ambient) measures that accounted for system drift. The entire gas analysis system was also periodically calibrated against gases of known concentrations. Rates of oxygen consumption were calculated for both the animal resting in dry ambient air conditions ($\dot{V}O_{2air}$) and while the animal was submerged in each one of the three different water temperatures ($\dot{V}O_{2water}$), using LabAnalystX software (http://warthog.ucr.edu/WartHogPage/FTPindex.html) and incorporating the appropriate equations from Withers (1977). The $\dot{V}O_{2air}$ and $\dot{V}O_{2water}$ were determined as the lowest continuous average oxygen consumption maintained for 10 min during the last 15 min of the dry phase and the last 25 min of the wet phase. A malfunctioning CA-1B analyzer (CO_2 sensor) was detected in a portion of the first two seasonal cycles of this study. For a few trials, with an average RQ value over the entire dry-wet metabolic session outside of a reasonable physiological range (0.65–1.05), $\dot{V}O_{2air}$ was calculated using a fixed RQ value of 0.8 rather than actual measures of expired CO_2.

Mass and Body Composition

The deuterium (D_2O) dilution technique was used once on each of the fur seals in each seasonal cycle to determine their total body water (Reilly and Fedak 1990). Body composition (total body lipid) was then estimated from the total body water using the "all animal–adult and pup" regression equation validated by Arnould *et al.* (1996) for Antarctic fur seals. Briefly, blood samples were obtained from the animals while under veterinary supervised anesthesia (maximum 5% isoflurane). An initial blood sample was drawn into a serum separator tube prior to the administration of the D_2O, such that the background levels of ^2H could be assessed. The injection of 99.9% D_2O was then administered intramuscularly at a measured dosage of approximately 0.16 g/kg of animal. A second blood sample was drawn 2 h after injection (permitting equilibration with the body water pool) to assess the increase in the concentration of ^2H. Animals were awake and kept in a holding run with a circular wading pool and running water during the 2 h equilibration period; this did not confound the calculation of total body water as these individuals have never been observed to drink water.

Blood samples were centrifuged and the collected serum was stored at −70°C until analysis. Metabolic Solutions Inc. (Nashua, NH) conducted the isotope analysis of the serum and dose samples, using a Europa Hydra continuous flow isotope ratio mass spectrometer and the methodology described by Scrimgeour *et al.* (1993). Body mass measurements of each fur seal (necessary for determining the proper dosage of D_2O and as a measurement of growth) were collected daily prior to the first injection and first feed (at least 16 h postprandial) by having the fur seal station on a platform scale (±0.02 kg).

Data Analysis

Seasonal changes in rates of oxygen consumption (metabolic rate) over the study period in either ambient air conditions or when immersed in water were determined using separate linear mixed effects (LME) models, with the random effect of the individual included to account for repeated measures. If significant differences were detected, we used a *post hoc* Tukey contrasts simultaneous test for general linear hypotheses to determine between which seasons the significant differences occurred. Additionally, LME models, with individual again as the random effect, were used to investigate the effects of either the ambient air or water temperatures on the appropriate metabolic rates throughout the year and within individual seasons. As ambient air temperature was found to be significantly affecting the mass-specific $\dot{V}O_{2air}$ in the winter, ambient air temperature was included as a covariate when testing the effects of water temperature on metabolic rate throughout the year and within individual seasons.

The potential costs of thermoregulation were determined as the paired difference between the dry ambient air and wet immersed mass-specific $\dot{V}O_2$ within an individual session. Innate rhythmicity is fundamental to a seasonal mammal's biology (Warner *et al.* 2010). Circadian oscillators regulate the day-night cycle of metabolic and behavioral processes, and photoperiod affects the annual rhythm of energy metabolism, molting, and reproduction (Warner *et al.* 2010). Therefore, this approach controlled for any variance in resting metabolism, which might obscure any real changes in metabolism due to costs of thermoregulation (*i.e.*, reduces Type II error). LME models, with the individual as the random effect, were used to investigate seasonal changes in the potential costs of thermoregulation over the course of the study. As season was found to be a significant predictor of the potential costs of thermoregulation, separate models within each season were also constructed to determine the effects of the water temperature on the potential costs of thermoregulation. If significant differences were detected, a *post hoc* Tukey contrasts simultaneous test for general linear hypotheses was used to determine between which temperatures the significant differences occurred. Single sample *t*-tests were used to determine if the potential costs of thermoregulation (*i.e.*, increase in metabolism) at any given temperature was significantly different than zero.

Seasonal changes over the study period in body mass, body composition, and their respective rates of change were also determined using LME models, with the random effect of the individual included to account for repeated measures. Again, if significant differences were detected, a *post hoc* Tukey contrasts simultaneous test for general linear hypotheses was used to determine between which seasons the significant differences occurred. All statistical analyses were conducted using the R software package (R Development Core Team 2012).

Sea Surface Temperature Encountered During the Annual Migration

Contour plots of the average sea surface temperatures (SST) were obtained for the Northeast Pacific Ocean by month (1982–2012) from Fisheries and Oceans Canada (http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/sst-tsm/index-eng.htm). Different iterations of the annual migration patterns of juvenile and adult female northern fur seals from North American rookeries were overlaid onto these contour plots. While the individual migratory studies covered various time periods from 1871 to 2006 (Kenyon and Wilke 1953, Bigg 1990, Gentry 1998, Ream *et al.* 2005, and Melin *et al.* 2012), there is a high degree of consistency between descriptions. Specifically, they considered time frames of 1955–1977 (Bigg 1990), 1871–1977 (Gentry 1998), 1871–1911 and 1940–1948 (Kenyon and Wilke 1953), 2002 (Ream *et al.* 2005), and 2006 (Melin *et al.* 2012). Combined, the contour plots and descriptions of the migration pattern allowed us to estimate the minimum and maximum average SST that juvenile female northern fur seals encountered during each month of their annual migration through the Bering Sea and North Pacific Ocean (Fig. 1, e.*g.,* month of November in 1982 with migration pattern as described by Ream *et al.* 2005).

RESULTS

Metabolic Rates in Ambient Air

Rates of oxygen consumption and other variables are presented as means ± 1 SD. The mean rate of oxygen consumption of the northern fur seals resting in dry ambient air conditions ($\dot{V}O_{2air}$) across all individuals and all seasons was 339.2 ± 148.6 mL O_2 min^{-1} which, on a mass-specific basis, was 17.6 ± 7.3 mL O_2 kg^{-1} min^{-1} (Table I).

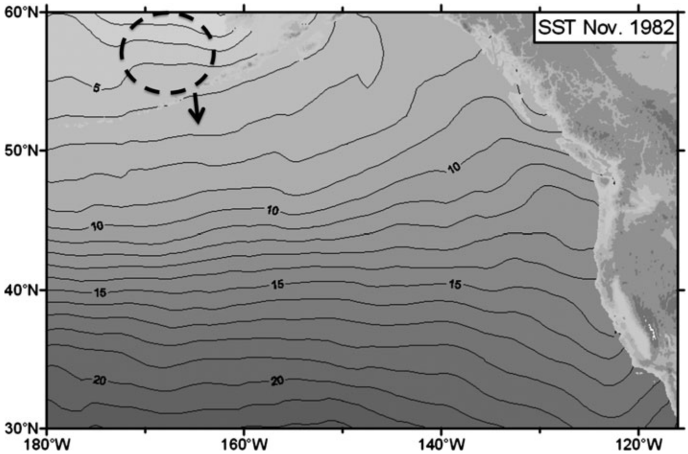

Figure 1. Example of the relationship between described locations of northern fur seals (within dotted zone and arrow) and monthly average sea surface temperature in November of 1982 (isocline bars in ºC). Fur seal locations are based on the annual migration pattern movement data from Ream *et al*. (2005), for northern fur seals from the Pribilof Islands during a single month (November). The presumed location during each month as based on the variously described migration patterns (see text) is plotted onto a contour map of the northeast Pacific Ocean displaying the sea surface water temperatures (SST) for that month of the region, for each year from 1982 to 2012 (data from Fisheries and Oceans Canada, http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/sst-tsm/index-eng.htm). Collective results are summarized in Fig. 5.

However, one individual (ME08) was unusually active during these trials, and yielded data that did not reflect resting conditions. Omitting the $\dot{V}O_{2air}$ data from this individual, the average mass-specific $\dot{V}O_{2air}$ of the remaining northern fur seals, across all seasons, was 15.4 ± 5.1 mL O_2 kg^{-1} min^{-1} (Table 1). This translated to an average in-air resting metabolic rate that was 3.2 times Kleiber's (1975) prediction for similar-sized adult terrestrial mammals. The average mass-specific $\dot{V}O_{2air}$ was significantly different among seasons ($P = 0.001$) and was significantly higher in the fall seasonal trials (19.3 ± 3.4 mL O_2 kg^{-1} min^{-1}; 4.2× Kleiber) compared to the other three seasonal trials (overall mean 14.1 ± 4.9 mL O_2 kg^{-1} min^{-1}; 2.9× Kleiber; $P = 0.005$), which did not differ significantly from one another ($P = 0.5$; Table 1).

Ambient air temperatures in the metabolic chamber during these trials did change significantly over the course of the study ($P = 0.001$). The highest average ambient air temperature of 13.0°C ± 3.4°C occurred during the summer trials, compared to the average ambient air temperatures of 8.6°C ± 2.3°C during the spring, 10.6°C ± 2.7°C during the fall and 6.6°C ± 4.3°C during the winter seasonal trials. Ambient air temperature, however, had no significant effect on the mass-specific $\dot{V}O_{2air}$ of the northern fur seals across all trials ($P = 0.4$), or within the spring, summer or fall seasons (ambient air temperatures range during spring, summer, and fall was 8°C–18°C; $P = 0.3$). Ambient air temperature significantly affected the mass-specific $\dot{V}O_{2air}$ in the winter ($P = 0.04$), with the mass-specific $\dot{V}O_{2air}$ appearing to increase at temperatures below 2.5 °C (Fig. 2). Removing the mass-specific $\dot{V}O_{2air}$ data measured in ambient air temperatures below 2.5°C, the average mass-specific $\dot{V}O_{2air}$ for

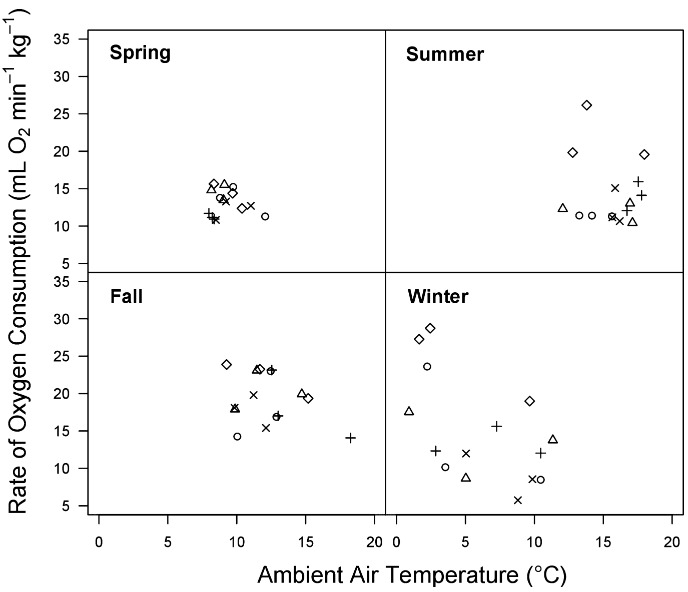

Figure 2. Seasonal mass-specific rates of oxygen consumption in ambient air (mL O_2 min^{-1} kg^{-1}) in comparison to the air temperatures at which the trials were conducted for five, 3 yr old female northern fur seals from March 2011 to January 2012. Individual symbols represent individual test subjects: AN08 (○), AY08 (Δ), KY08 (+), TI08 (×), and TU08 (◊). In the winter, the mass-specific $\dot{V}O_{2air}$ appears to increase at temperatures below 2.5 °C.

the winter trials decreased to 11.4 ± 3.9 mL O_2 kg^{-1} min^{-1}, yet the overall seasonal trend in the mass-specific $\dot{V}O_{2air}$ did not change (*i.e.*, fall metabolism was higher than all other seasons).

Metabolism during Wet Thermal Challenges

The mean rate of oxygen consumption of the northern fur seals across all individuals (omitting individual “ME08”) and all tested water temperatures was 17.5 ± 5.1 mL O_2 kg^{-1} min^{-1} while resting immersed in water ($\dot{V}O_{2water}$); equivalent to 341.6 ± 108.6 mL O_2 min^{-1}). As with $\dot{V}O_{2air}$, the mass-specific rate of oxygen consumption while resting immersed in water differed significantly between seasons ($P = 0.001$). Within the individual seasons, no difference in the mass-specific $\dot{V}O_{2water}$ was attributable to water temperature in the spring, summer, and fall seasonal trials ($P = 0.1$). However, water temperature was a significant predictor of the mass-specific $\dot{V}O_{2water}$ during the winter ($P = 0.02$). The inclusion of ambient air temperature as a covariate into the linear mixed effects models found ambient air temperature to be a significant predictor of the mass-specific $\dot{V}O_{2water}$ in the winter ($P = 0.01$). As a result of including ambient air temperature, no difference in the mass-specific $\dot{V}O_{2water}$ was attributable to water temperature in the winter either ($P = 0.9$; Fig. 3).

We controlled for variance in resting metabolic rates associated with circadian oscillators and photoperiodic affects by calculating the paired difference between the dry ambient air and wet immersed mass-specific $\dot{V}O_2$ within an individual session. Overall, water temperature was not significant in the paired difference between the

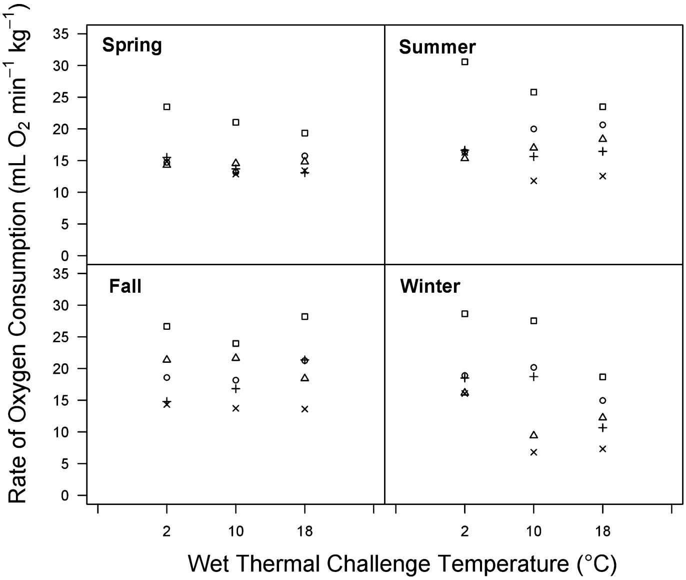

Figure 3. Seasonal in water mass-specific rates of oxygen consumption (mL O_2 min^{-1} kg^{-1}) in comparison to the three water temperatures (2°C, 10°C, and 18°C) at which the trials were conducted for five, 3 yr old female northern fur seals from March 2011 to January 2012. Individual symbols represent individual test subjects: AN08 (○), AY08 (Δ), KY08 (+), TI08 (×), and TU08 (□). The inclusion of ambient air temperature as a covariate into the linear mixed effects models found ambient air temperature to be a significant predictor of the mass-specific $\dot{V}O_{2water}$ in the winter and therefore no difference in the mass-specific $\dot{V}O_{2water}$ was attributable to water temperature in any season.

dry ambient air and wet immersed mass-specific $\dot{V}O_2$ within an individual session in any of the seasonal trials (Fig. 4). The cost of thermoregulation at each water temperature within each season was not significantly different from zero within each seasonal trial ($P = 0.06$), with the exception of the summer seasonal trials ($P = 0.02$). During the summer seasonal trials, the paired difference within an individual session between the $\dot{V}O_{2air}$ and $\dot{V}O_{2water}$ at 2°C was significantly different from zero ($P = 0.04$). For these trials, the mass-specific $\dot{V}O_{2water}$ was 19.0 ± 6.5 mL O_2 kg^{-1} min^{-1} which was 36% higher on average than the associated $\dot{V}O_{2air}$.

Mass and Body Composition

Over the course of the study, the average body mass of the individual fur seals increased significantly by 3.9 kg ($P = 0.001$). The average body mass was lowest during the spring trials (16.7 ± 2.5 kg), significantly higher in the subsequent summer trials (19.3 ± 2.5 kg; $P = 0.001$), and higher again in the fall trials, when the average body mass was highest (21.2 ± 2.8 kg; $P = 0.003$). While the average body mass was slightly lower (but not significantly different) during the winter trials (20.6 ± 2.5 kg; $P = 0.7$), it was still significantly higher in the winter than in the spring ($P = 0.001$; Table 1).

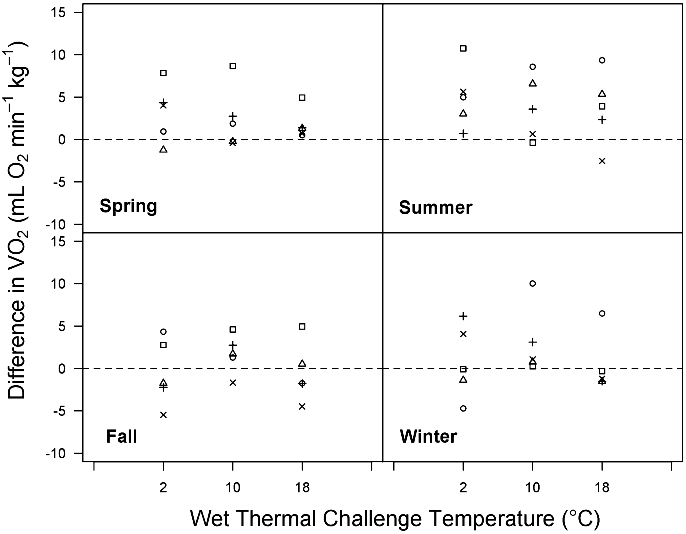

Figure 4. Seasonal potential costs of thermoregulation for five, 3 yr old female northern fur seals (from March 2011 to January 2012), controlling for variance in resting metabolic rates—determined as the paired difference between the dry ambient air and wet immersed mass-specific $\dot{V}O_2$ within an individual session (mL O_2 min^{-1} kg^{-1}). Data are presented for each of the three wet thermal challenge temperatures (2°C, 10°C, and 18°C). Individual symbols represent individual test subjects: AN08 (○), AY08 (Δ), KY08 (+), TI08 (×), and TU08 (□). The cost of thermoregulation was not significantly different from zero within each seasonal trial for any water temperature, with the exception of the 2°C thermal challenge in the summer seasonal trial.

Within the seasonal trials, the individual's growth rates (standardized as changes in the absolute body mass over the course of an entire 6 wk seasonal trial) were significantly positive during both the spring (P = 0.03) and summer trials (P = 0.04), while there were no significant changes in body mass during the fall (P = 0.1) and winter trials (P = 0.08).

The average absolute amount of lipid in the fur seals' bodies also significantly increased by 1.5 kg over the course of the study period (from 0.7 ± 0.3 kg to 2.3 ± 0.8 kg; P = 0.001), and the rate of increase in lipids was constant between the seasons (P = 0.2). The percent body mass that was lipid also increased constantly throughout the year (as would be predicted for growing animals), such that our study animals had the lowest absolute and relative amount of lipids during the spring trials (0.7 kg or 4.6% ± 2.1% of total body mass) and the highest absolute and relative amount of lipids during the winter trials (2.3 kg or 11.0% ± 3.7% of body mass).

Average Sea Surface Temperature (SST)

Estimates of the minimum and maximum average sea surface temperature encountered over the course of the fur seals' annual migration included high variability resulting from the spatial and temporal uncertainty of the exact location of female and juvenile individuals in the population (of the Pribilof Islands and Bogoslof

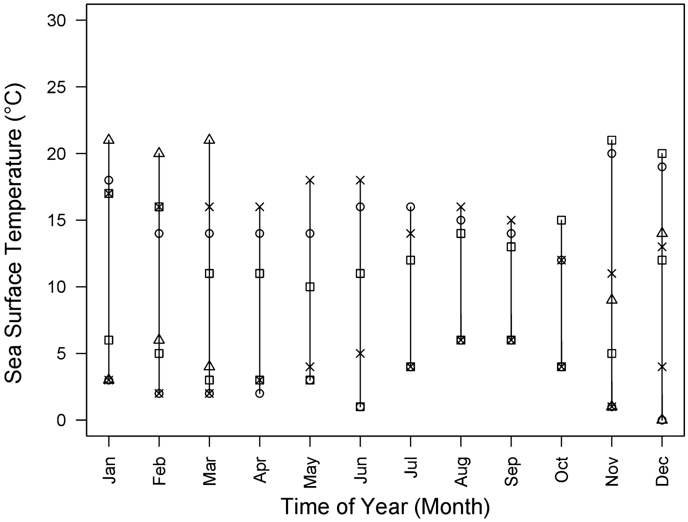

Figure 5. Range of average sea surface temperatures in degree Celsius (between 1982 and 2012) that adult female and juvenile northern fur seals from the Pribilof Islands and Bogoslof Island, Alaska are likely exposed to each month if they followed the migratory patterns described by Bigg (1990, ×), Gentry (1998, □), Kenyon and Wilke (1956, ○) and Ream *et al.* (2005, Δ). Individual symbols represent the maximum and minimum temperatures obtained from each of the migratory pattern iterations.

Island) at different times of the year. This is represented in the different migratory routes and timings variously described by Kenyon and Wilke (1953), Bigg (1990), Gentry (1998), and Ream *et al.* (2005). Mild variation also resulted from the interannual spatial changes in SST throughout the Northeast Pacific Ocean for each month of the year from 1982 to 2012.

Average SST in the central and southern Bering Sea range from as low as 0°C to as high as 14°C between late May and late December when fur seals are present. However, adult females and juveniles encounter warmer water temperatures as they move southward through the Aleutian Islands into the North Pacific Ocean. The individuals then spread out and move over deep water en route to the wintering areas: either the transitional region of the central North Pacific Ocean or along the continental margins of North America from California to Sitka, Alaska. The northward return migration begins in early spring, as individuals move in a loose aggregation along the continental margins or offshore and eventually cross the Gulf of Alaska and the North Pacific Ocean to re-enter the Bering Sea. Most breeding individuals return to the Pribilof Islands in late May or June. Over the 8–10 mo migration, individuals can encounter SST as low as 2°C–3°C just south of the Aleutian Islands and in the Gulf of Alaska in January through May and as high as 19°C–21°C off the coast of southern California or in the southern transition zone of the North Pacific Ocean in November through March (Fig. 5).

In comparison to fur seals that breed in the Bering Sea, females breeding in California remain near the continental margins of North America and shift their at-sea distribution northwards and offshore in the winter (Melin *et al.* 2012). As a result, the average SST encountered by female members of this population appear to stay within the range of 8°C–20°C, with little variation throughout the year.

DISCUSSION

The in-air metabolic rate of the northern fur seals in our study was equivalent to 3.2 times Kleiber's (1975) allometric prediction for adult mammals, which is consistent with other studies of northern fur seals that ranged in age from postmolt pups to 5 yr of age (Miller 1978, Donohue *et al.* 2000). As individuals develop, the mass-specific metabolic rate would generally be expected to decrease, due to reductions in the cost of growth as well as the allometric effects of increased absolute body mass (Kleiber 1975, Boyd 2002). Yet, within this general trend, seasonal variation would be expected due to changes in overall energy budgets (Robeck *et al.* 2001, Rosen *et al.* 2012).

Metabolism was highest in our study during the fall seasonal trials, but this was unlikely due to the costs of higher growth rates or a product of absolute body size. Absolute body mass was highest in the fall, but growth rates were higher during the spring and summer trials than during the fall or winter trials. In addition, the mass-specific $\dot{V}O_{2air}$ from the winter to summer periods did not differ significantly between seasons, unlike the absolute body size of the individuals, which did change significantly.

We also found no evidence that the seasonal changes in the metabolic rate were related to thermoregulatory costs, as there was no relationship between the measured metabolic rates and ambient air temperatures within or between sets of trials, except during the winter seasonal trials. During the winter, the mass-specific $\dot{V}O_{2air}$ appeared to increase with ambient air temperatures below 2.5°C. Comparatively, a previous study of juvenile (2–5 yr old) northern fur seals failed to find metabolic changes across air temperatures of ~−1°C–18°C (Miller 1978). A different study, reported a lower critical air temperature for newborn northern fur seal pups between 0°C and 4°C (Blix *et al.* 1979). On the Pribilof Islands (the location of the main breeding colony, Towell *et al.* 2008), documented average air temperatures below 2.5°C only occurred between November and April (1956–1986) when female and juvenile northern fur seals are generally undertaking their annual pelagic migration (Trites and Antonelis 1994). Therefore, the suggested lower critical air temperature of our study supports the hypothesis that reduced air temperatures, in conjunction with increasing storm occurrences and winds speeds, which destroy a pelage's insulating air layer, are responsible for initiating the annual pelagic migration of these individuals (Trites and Antonelis 1994, Lea *et al.* 2009).

Molting, noted to be an energetically expensive process, is the most logical explanation for the elevated metabolic rate we observed in the fall (Boyd *et al.* 1993). Northern fur seals entering their third year (such as our study animals) have their molt centered in September (Scheffer 1962), which coincided with our fall trials. The 50% increase in metabolic rate exhibited by our fur seals in the fall relative to the other seasons was comparable to the 30%–87% increase in metabolism associated with the molt in Steller and California sea lions (*Eumetopias jubatus* and *Zalophus californianus*; Kumagai 2004, Williams *et al.* 2007).

Molting is believed to decrease thermoregulatory capacity and add an additional energetic cost for many species of marine mammals (Boyd *et al.* 1993, Boily 1995). This could be substantial for northern fur seals, which take 4 or 5 mo to molt and rely primarily on their pelage for insulation (Scheffer 1962; Liwanag *et al.* 2012*a*, *b*). However, we found that juvenile female northern fur seals in our study did not incur any additional energetic costs to being submerged in water (at any temperature) during the fall seasonal trails. This lack of thermoregulatory cost during the molt might be because northern fur seals do not lose old hairs until new replacement hairs have emerged (Scheffer 1962).

Similar to a lack of thermoregulatory cost during the fall seasonal trials, there was no increase in metabolic rates between the dry and wet conditions in any of the seasonal trials with the exception of the summer seasonal trials for the 2°C water temperatures. While our study found a lack of thermal costs at three specific water temperatures (2°C, 10°C, and 18°C), it is logical to assume that the same was true at the intermediary water temperatures. Thus, while we identified a zone of thermal neutrality—a portion of the overall TNZ—we failed to identify specific upper or lower critical water temperatures.

Our failure to detect an upper critical water temperature in any season was not surprising given that it is energetically inexpensive for marine mammals to dissipate excess heat in water (Williams and Worthy 2002). Otariids have specialized blood vessels (arteriovenous anastomoses) in their flippers that can readily dissipate excess heat through the skin surface while swimming (Bryden and Molyneux 1978, Williams and Worthy 2002). To date, only one study has found an upper critical water temperature (UCT) of 8°C, and it was only during a single set of trials with younger northern fur seals (Rosen and Trites, in press). Comparatively, Liwanag (2010) could not identify an UCT in northern fur seal pups exposed to water temperatures as high as 25°C.

In terms of the lower critical water temperature (LCT), we presume it is below or near to the 2°C water temperatures we tested, which is lower than what we had predicted based on studies of other aquatic and semiaquatic mammals that depend on a dense pelage for thermoregulation (Dawson and Fanning 1981, Costa and Kooyman 1982, Williams 1986, Rutishauser *et al.* 2004). Previous studies of younger northern fur seals immersed in water had reported LCTs ranging from 3.9°C–6.5°C (Rosen and Trites, in press), to 8.3°C ± 2.5°C (Liwanag 2010), to ~10°C (postmolt, preweaning pups; Donohue *et al.* 2000). It is noteworthy that all of these previous studies were undertaken with slightly different age groups. One other study that did use northern fur seals of similar ages to those we studied had a reported LCT in water of >18°C (Miller 1978). However, this surprisingly high value may be confounded by the costs of diving, grooming, and swimming that occurred throughout the trials, as costs of movement can be substantial (Darveau *et al.* 2002).

Comparing the reported LCTs of other studies to our finding that it is near to or below 2°C for juvenile females suggests that the apparent differences between the various studies may reflect a general decrease in LCT with age (Miller 1978, Donohue *et al.* 2000, Liwanag 2010, Rosen and Trites, in press). Energetically, developing a broad thermal neutral zone and explicitly a lower LCT may be necessary prior to bearing any additional energetic costs associated with reproduction and lactation, which for the northern fur seal occurs with maturation between the ages of 3 and 7 yr old (Williams *et al.* 2007, COSEWIC 2010).

It is not immediately obvious how northern fur seals could have a LCT near to or below 2°C when the sea otter, with a pelage containing many similar morphological traits but twice as dense, has a reported LCT of 20°C (Costa and Kooyman 1982, Williams *et al.* 1992; Liwanag *et al.* 2012*a*, *b*). The difference between species does not appear to be due to difference in surface area, as our fur seals (which increased in mass from 16.7 to 20.6 kg over the course of our study) would have had a calculated surface area of 0.52–0.60 m^2 (Irving *et al.* 1935, Blix *et al.* 1979, Innes *et al.* 1990, Trites 1990), which is similar to the estimated surface area of 0.50–0.81 m^2 for 16.6–20.0 kg sea otters (Costa and Kooyman 1982). Nor does it seem that our fur seals obtained increased insulation from their minimal blubber layer (average fat layer at birth is 2–4 mm, and 1.8–3.8 mm for captive 3 yr olds; Blix *et al.* 1979; DASR, unpublished data), in comparison to the sea otter's lack of a blubber layer (Davis *et al.* 1988).

Blubber is a relatively poor insulator, requiring high amounts and thick layers to establish effective insulation. Phocid seals, which depend primarily on blubber to minimize heat loss to the environment, have an average layer of ~40 mm—over 10 times thicker than in our fur seals (Scholander *et al.* 1950, Liwanag *et al.* 2012*a*). In our study, the absolute and relative amount of lipid mass of the fur seals increased over the course of the trials. However, having higher relative lipid layers would be more beneficial for thermoregulation in younger rather than older animals because smaller individuals have higher surface area to body mass ratios (Arnould *et al.* 1996, Willmer *et al.* 2005). Thus, the change in lipid we observed was likely developmental or allometric in nature.

A potential explanation for the differences in LCT between sea otters and northern fur seals might be attributable to differences in several key features in their pelage, specifically the density of the guard hairs and the quantity of sebaceous glands present (Scheffer 1962, Williams *et al.* 1992). While sea otters possess higher absolute density of hairs, the density of guard hairs in the northern fur seal's pelage is ~20%–90% greater (1,425–2,280 hairs/cm^2; between 2.5% and 4% of the total fur seal hairs) than for the sea otter (990–1,200 hairs/cm^2) (Scheffer 1962, Williams *et al.* 1992). Although guard hairs are believed to provide little insulation themselves, associated with each guard hair follicle are sebaceous glands that provide a hydrophobic barrier against pelage wetting through the excretion of sebum, a mixture of nonpolar lipids (Irving *et al.* 1962, Williams *et al.* 1992). The sea otter has a single, large, bi-lobed sebaceous gland (Williams *et al.* 1992), while the northern fur seal in contrast has a pair of round sebaceous glands subdivided into two or three lobes for each guard hair follicle (Scheffer 1962). The northern fur seal could therefore have 2.4–3.8 times as many sebaceous glands compared to the sea otter. While the sebum composition is extremely species-specific (Zouboulis 2004) and an increased number of sebaceous glands does not necessarily equate to a greater volume of sebaceous secretions, this anatomical difference might explain why the northern fur seal has a broader TNZ than the sea otter.

The unpredicted resiliency of juvenile female northern fur seals to the effect of environmental water temperatures on metabolic rates would also suggest that the migration of juvenile female northern fur seals might not be constrained by water temperatures as commonly believed. Our investigation of the average sea surface temperatures encountered by northern fur seals in the Bering Sea and North Pacific Ocean during their annual migration (as described by Gentry 1998) suggests that they generally stay within a narrow range of temperatures from March to September, but experience higher, more variable water temperatures in the months of November to February. However, the migration patterns described by Kenyon and Wilke (1953), Bigg (1990) and Ream *et al.* (2005) suggests fur seals encounter greater variability of the average SST throughout their migration—and that they exploit their entire broad zone of thermal neutrality from November to June. The relatively narrow range of water temperatures they experience from July to October occurs predominantly in the Bering Sea and likely reflects a geographic aggregation for breeding where food is plentiful and survival of newborns is high, rather than a direct response to thermal conditions imposed by water temperatures (Trites 1990, Trites and Antonelis 1994).

The wide thermal neutral zone we observed implies that northern fur seals predominantly do not have to increase their metabolism to maintain a constant core body temperature while foraging or resting at sea, although changes in temperature with depth or the effect of microclimates cannot be discounted (Williams and Worthy 2002). Vertical oceanographic thermal properties, critical to the foraging success of the northern fur seal, can produce subsurface water temperatures as low as −2°C (the freezing point of sea water) during dives (Kuhn 2011). Nevertheless, thermal substitution, the use of heat produced during activity or the processing of food, in combination with relatively short dive durations could minimize any additional energetic disadvantage associated with diving to depth (Lovvorn 2007; Liwanag *et al.* 2009, 2010; Kuhn 2011).

Ecologically, a broad thermal neutral zone implies that prey choice for juvenile females should not be limited by thermal considerations because they have the thermal capacity to alter their migration in response to changes in prey availability and distribution. Migration patterns of the northern fur seal were undoubtedly first established by moving between seasonal prey aggregations that provided predictable energetic resources (Sigler *et al.* 2009). Northern fur seals consume over 70 different species of fish, cephalopods, and crustaceans (Perez and Bigg 1986, Newsome *et al.* 2007, COSEWIC 2010) and presumably take advantage of seasonal pulses and spatial aggregations of prey (energy resources) during their annual migration (Perez and Bigg 1986, Lowry *et al.* 1991).

However, the broad distribution of northern fur seals across the North Pacific does not mean that northern fur seal behavior is unaffected by thermal considerations. While abrupt changes in weather conditions (*e.g.*, increase in storm frequency, extent of ice cover) beginning in November are hypothesized to be an impetus to migration (Trites and Antonelis 1994, Lea *et al.* 2009), lower water temperatures likely also play a role. Females and juvenile northern fur seals are absent from the Bering Sea between January and May, when average sea surface water temperatures range between 0°C and 4°C. Individuals that remain in the Bering Sea during this time would likely experience an added energetic expense that depletes energy reserves, hinders growth and reproduction, and may ultimately lead to starvation (Rutihauser *et al.* 2004, Lea *et al.* 2009).

In comparison to fur seals that breed in Alaska, females from San Miguel Island remain near the continental margins of North America throughout the year, encountering a generally higher and constant range of temperatures (general temperature exposure range was 8°C–20°C) due to the year-round upwelling of the California Current waters off southern California (Melin *et al.* 2012). Upwelling effects tend to be stronger in the summer, but change from day to day with wind speed and direction (Mann and Lazier 1991). Overall, this year-round upwelling constantly brings new nutrients to the water surface and appears to provide a productive ecosystem for a finite number of northern fur seals year round, such as the individuals from San Miguel Island or historical populations from mainland California and Oregon (Mann and Lazier 1991, Burton *et al.* 2001).

Despite their wide at-sea distribution in the North Pacific Ocean, northern fur seals (female and juvenile individuals) do not appear to migrate to waters that exceed 21°C, suggesting there may be an upper critical water temperature (although one has yet to be identified). Northern fur seals (juvenile female individuals) nevertheless have an impressively wide zone of thermal neutrality (spanning at least near to or below 2°C–18°C based on our measurements), and are physiologically well equipped to exploit the entire Bering Sea and North Pacific Ocean.

Acknowledgments

We thank the research and husbandry staff of the Vancouver Aquarium and the Marine Mammal Energetics and Nutrition Laboratory for their assistance throughout this study; and extend our thanks to T. Dalton, B. Wright, V. Noble, Dr. W. K. Milsom, and two anonymous reviews for providing valuable feedback. Funding was provided by the National Oceanic and Atmospheric Administration through the North Pacific Marine Science Foundation to the North Pacific Universities Marine Mammal Research Consortium. Animal Care Committees of both the Vancouver Aquarium and the University of British Columbia (Permit #A10-0342) approved all animal use and research protocols.

Literature Cited

Angilletta, M. J. 2009. Thermal adaptation: A theoretical and empirical synthesis. Oxford University Press, Oxford, U.K.

Arnould, J. P. Y., I. L. Boyd and J. R. Speakman. 1996. Measuring the body composition of Antarctic fur seals (*Arctocephalus gazella*): Validation of hydrogen isotope dilution. Physiological Zoology 69:93–116.

Bigg, M. A. 1990. Migration of northern fur seals (*Callorhinus ursinus*) off western North America. Canadian Technical Report of Fisheries and Aquatic Sciences 1764. 64 pp.

Blix, A. S., L. K. Miller, M. C. Keyes, H. J. Grav and R. Elsner. 1979. Newborn northern fur seals (*Callorhinus ursinus*)—do they suffer from the cold? American Journal of Physiology 236:322–327.

Boily, P. 1995. Theoretical heat flux in water and habitat selection of phocid seals and beluga whales during the annual molt. Journal of Theoretical Biology 172:235–244.

Boyd, I. L. 2002. Energetics: Consequences for fitness. Pages 247–277 *in* A. R. Hoelzel, ed. Marine mammal biology: An evolutionary approach. Blackwell Science Inc., Malden, MA.

Boyd, I. L., T. Arnbom and M. Fedak. 1993. Water flux, body composition, and metabolic rate during molt in female southern elephant seals (*Mirounga leonina*). Physiological Zoology 66:43–60.

Bryden, M. M., and G. S. Molyneux. 1978. Arteriovenous anastomoses in the skin of seals II. The California sea lion *Zalophus californianus* and the northern fur seal *Callorhinus ursinus* (Pinnipedia: Otariidae). Anatomical Record 191:253–260.

Burton, R. K., J. J. Snodgrass, D. Gifford-Gonzalez, T. Guilderson, T. Brown and P. L. Koch. 2001. Holocene changes in the ecology of northern fur seals: Insights from stable isotopes and archaeofauna. Oecologia 128:107–115.

COSEWIC. 2010. COSEWIC assessment and status report on the northern fur seal *Callorhinus ursinus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada. 50 pp. Available at http://www.sararegistry.gc.ca/status/status_e.cfm.

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*. Canadian Journal of Zoology 60:2761–2767.

Darveau, C. A., R. K. Suarez, R. D. Andrews and P. W. Hochachka. 2002. Allometric cascade as a unifying principle of body mass effects on metabolism. Nature 417:166–170.

Davis, R. W., T. M. Williams, J. A. Thomas, R. A. Kastelein and L. H. Cornell. 1988. The effects of oil contamination and cleaning on sea otters (*Enhydra lutris*). II. Metabolism, thermoregulation, and behavior. Canadian Journal of Zoology 66:2782–2790.

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. Physiological Zoology 54:285–296.

Dejours, P. 1987. Water and air: Physical characteristics and their physiological consequences. Pages 3–11 *in* P. Dejours, L. Bolis, C. R. Taylor and E. R. Weibel, eds. Comparative physiology: Life in water and on land. Springer-Verlag, New York, NY.

DeLong, R. L. 1982. Population biology of northern fur seals at San Miguel Island, California. Ph.D. dissertation, University of California, Berkeley, CA. 185 pp.

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. Journal of Experimental Biology 203:1003–1016.

Gentry, R. L. 1998. Behavior and ecology of the northern fur seal. Princeton University Press, Princeton, NJ.

Gordon, M. S., G. A. Bartholomew, A. D. Grinnell, C. B. Jorgensen and F. N. White. 1972. Animal physiology: Principles and adaptations. The Macmillan Company, New York, NY.

Hurley, J. A., and D. P. Costa. 2001. Standard metabolic rate at the surface and during trained submersions in adult California sea lions (*Zalophus californianus*). Journal of Experimental Biology 204:3273–3281.

Innes, S., G. A. J. Worthy, D. M. Lavigne and K. Ronald. 1990. Surface area of phocid seals. Canadian Journal of Zoology 68:2531–2538.

Irving, I., L. J. Peyton, C. H. Bahn and R. S. Peterson. 1962. Regulation of temperature in fur seals. Physiological Zoology 35:275–284.

Irving, L., and J. S. Hart. 1957. The metabolism and insulation of seals as bare-skinned mammals in cold water. Canadian Journal of Zoology 35:497–511.

Irving, L., D. M. Solandt, S. D. Y and F. C. Fisher. 1935. The respiratory metabolism of the seal and its adjustment to diving. Journal of Cellular and Comparative Physiology 7:137–151.

Kasting, N. W., S. A. L. Adderley, T. Safford and K. G. Hewlett. 1989. Thermoregulation in beluga (*Delphinapterus leucas*) and killer (*Orcinus orca*) whales. Physiological Zoology 62:687–701.

Kenyon, K. W., and F. Wilke. 1953. Migration of the northern fur seal, *Callorhinus ursinus*. Journal of Mammalogy 34:86–98.

Kleiber, M. 1975. The fire of life: An introduction to animal energetics. R. E. Kteiger Publishing Co., Huntington, NY.

Kuhn, C. E. 2011. The influence of subsurface thermal structure on the diving behavior of northern fur seals (*Callorhinus ursinus*) during the breeding season. Marine Biology 158:649–663.

Kumagai, S. 2004. Seasonal differences in physiology of captive Steller sea lions (*Eumetopias jubatus*) in response to short-term low energy intake. M.Sc. thesis, University of British Columbia, Vancouver, Canada. 95 pp.

Lea, M. A., D. Johnson, R. Ream, J. Sterling, S. Melin and T. Gelatt. 2009. Extreme weather events influence dispersal of naive northern fur seals. Biological Letters 5:252–257.

Liwanag, H. E. M. 2010. Energetic costs and thermoregulation in northern fur seal (*Callorhinus ursinus*) pups: The importance of behavioural strategies for thermal balance in furred marine mammals. Physiological and Biochemical Zoology 83:898–910.

Liwanag, H. E. M., T. M. Williams, D. P. Costa, S. B. Kanatous, R. W. Davis and I. L. Boyd. 2009. The effects of water temperature on the energetic costs of juvenile and adult California sea lions (*Zalophus californianus*): The importance of skeletal muscle thermogenesis for thermal balance. Journal of Experimental Biology 212:3977–3984.

Liwanag, H. E. M., A. Berta, D. P. Costa, M. Abney and T. M. Williams. 2012*a*. Morphological and thermal properties of mammalian insulation: The evolution of fur for aquatic living. Biological Journal of the Linnean Society 106:926–939.

Liwanag, H. E. M., A. Berta, D. P. Costa, S. Budge and T. M. Williams. 2012*b*. Morphological and thermal properties of mammalian insulation: The evolutionary transition to blubber in pinnipeds. Biological Journal of the Linnean Society 107:774–787.

Loughlin, T. R., and R. V. Miller. 1989. Growth of the northern fur seal colony on Bogoslof Island, Alaska. Arctic 42:368–372.

Lovvorn, J. R. 2007. Thermal substition and aerobic efficiency: Measuring and predicting effects of heat balance on endotherm diving energetics. Philosophical Transactions of The Royal Society B 362:2079–2093.

Lowry, M. S., B. S. Stewart, C. B. Heath, P. K. Yochem and J. M. Francis. 1991. Seasonal and annual variability in the diet of California sea lions *Zalophus californianus* at San Nicolas Island, California, 1981–86. Fishery Bulletin 89:331–336.

Mann, K. H., and J. R. N. Lazier. 1991. Dynamics of marine ecosystems biological: Physical interactions in the ocean. Blackwell Scientific Publications, Boston, MA.

Melin, S., J. Sterling, R. Ream, *et al*. 2012. A tale of two stocks: Studies of northern fur seals breeding at the northern and southern extent of the range. Alaska Fisheries Science Center, Research Feature: April/May/June 2012.

Miller, L. K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. U.S. Marine Mammal Commission, Report No. MMC-75/08. 27 pp.

Newsome, S. D., M. A. Etnier, C. M. Kurle, J. R. Waldbauer, C. P. Chamberlain and P. L. Koch. 2007. Historic decline in primary productivity in western Gulf of Alaska and eastern Bering Sea: Isotopic analysis of northern fur seal teeth. Marine Ecology Progress Series 332:211–224.

Perez, M. A., and M. A. Bigg. 1986. Diet of northern fur seals, *Callorhinus ursinus*, off western North America. Fishery Bulletin 84:957–971.

R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ream, R. R., J. T. Sterling and T. R. Loughlin. 2005. Oceanographic features related to northern fur seal migratory movements. Deep-Sea Research Part II: Topical Studies in Oceanography 52:823–843.

Reilly, J. J., and M. A. Fedak. 1990. Measurement of the body composition of living gray seals by hydrogen isotope dilution. Journal of Applied Physiology 69:885–891.

Robeck, T. R., S. Atkinson and F. Brook. 2001. Reproduction. Pages 193–236 *in* L. A. Dierauf and F. M. D. Gulland, eds. CRC handbook of marine mammal medicine. CRC Press, Boca Raton, FL.

Rosen, D. A. S., and A. W. Trites. In press. Thermal limits in young northern fur seals, *Callorhinus ursinus*. Marine Mammal Science doi: 10.1111/mms.12097.

Rosen, D. A. S., B. L. Young and A. W. Trites. 2012. Rates of maximum food intake in young northern fur seals (*Callorhinus ursinus*) and the seasonal effects of food intake on body growth. Canadian Journal of Zoology 90:61–69.

Rutishauser, M. R., D. P. Costa, M. E. Goebel and T. M. Williams. 2004. Ecological implications of body composition and thermal capabilities in young Antarctic fur seals (*Arctocephalus gazella*). Physiological and Biochemical Zoology 77:669–681.

Scheffer, V. B. 1962. Pelage and surface topography of the northern fur seal. North American Fauna 64:1–206.

Scholander, P. F., V. Walters, R. Hock and L. Irving. 1950. Body insulation of some arctic and tropical mammals and birds. Biological Bulletin (Woods Hole) 99:225–236.

Scrimgeour, C. M., M. M. Rollo, M. K. T. Mudambo, L. L. Handley and S. J. Prosser. 1993. A simplified method for deuterium/hydrogen isotope ratio measurements on water samples of biological origin. Biological Mass Spectrometry 22:383–387.

Sigler, M. F., D. J. Tollit, J. J. Vollenweider, *et al.* 2009. Steller sea lion foraging response to seasonal changes in prey availability. Marine Ecology Progress Series 388:243–261.

Strandberg, U., A. Kakela, C. Lydersen, *et al.* 2008. Stratification, composition, and function of marine mammal blubber: The ecology of fatty acids in marine mammals. Physiological and Biochemical Zoology 81:473–485.

Testa, J. W., ed. 2011. Fur seal investigations, 2008–2009. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-226. 80 pp.

Towell, R. G., R. R. Ream, C. W. Fowler and J. T. Sterling. 2008. Population assessment of northern fur seals on the Pribilof Islands, Alaska, 2006–2007. Pages 8–25 *in* J. W. Testa, ed. 2008. Fur seal investigations, 2006-2007. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-188. 76 pp.

Trites, A. W. 1990. Thermal budgets and climate spaces: The impact of weather on the survival of Galapagos (*Arctocephalus galapagoensis* Heller) and northern fur seal pups (*Callorhinus ursinus* L.). Functional Ecology 4:753–768.

Trites, A. W., and G. A. Antonelis. 1994. The influence of climatic seasonality on the life cycle of the Pribilof northern fur seal. Marine Mammal Science 10:311–324.

Warner, A., P. H. Jethwa, C. A. Wyse, H. I'anson, J. M. Brameld and F. J. P. Ebling. 2010. Effects of photoperiod on daily locomotor activity, energy expenditure, and feeding behavior in a seasonal mammal. American Journal of Physiology–Regulatory. Integrative and Comparative Physiology 298:R1409–R1416.

Williams, T. M. 1986. Thermoregulation of the North American mink during rest and activity in the aquatic environment. Physiological Zoology 59:293–305.

Williams, T. M., and G. A. J. Worthy. 2002. Anatomy and physiology: The challenge of aquatic living. Pages 73–97 *in* A. R. Hoelzel, ed. Marine mammal biology: An evolutionary approach. Blackwell Science Inc., Malden, MA.

Williams, T. D., D. D. Allen, J. M. Groff and R. L. Glass. 1992. An analysis of California sea otter (*Enhydra lutris*) pelage and integument. Marine Mammal Science 8:1–18.

Williams, T. M., J. E. Haun, R. W. Davis, L. A. Fuiman and S. Kohin. 2001. A killer appetite: Metabolic consequences of carnivory in marine mammals. Comparative Biochemistry and Physiology Part A Molecular and Integrative Physiology 129:785–796.

Williams, T. M., M. R. Rutishauser, B. Long, *et al.* 2007. Seasonal variability in otariid energetics: Implications for the effects of predators on localized prey resources. Physiological and Biochemical Zoology 80:433–443.

Willmer, P., G. Stone and I. Johnston. 2005. Environmental physiology of animals. 2nd edition. Blackwell Publishing, Malden, MA.

Withers, P. C. 1977. Measurement of VO_2, VCO_2, and evaporative water loss with a flow-through mask. Journal of Applied Physiology 42:120–123.

Zouboulis, C. C. 2004. Acne and sebaceous gland function. Clinics in Dermatology 22:360–366.

Received: 16 December 2012
Accepted: 28 October 2013