



Thermal limits in young northern fur seals, *Callorhinus ursinus*

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ABSTRACT

The thermoregulatory abilities of northern fur seals (*Callorhinus ursinus*) during their first two years in the frigid waters of the North Pacific Ocean may limit their geographic distribution and alter the costs for exploiting different species of prey. We determined the thermoneutral zone of six young northern fur seals by measuring their metabolism in ambient air and controlled water temperatures (0°C–12°C) from ages 8 to 24 mo. We found that the ambient air temperatures within our study (overall 1.5°C–23.9°C) did not affect resting metabolic rates. Calculated lower critical temperatures in water varied between 3.9°C and 8.0°C, while an upper critical temperature in water was only discernible during a single set of trials. These thermal responses provide insight into the possible physiological constraints on foraging ecology in young northern fur seals, as well as the potential energetic consequences of ocean climate change and altered prey distributions.

Key words: northern fur seal, *Callorhinus ursinus*, thermoregulation, metabolism, bioenergetics.

Young otariids (fur seals and sea lions) face a number of physiological challenges in the marine environment, including high potential thermoregulatory demands imposed by the physics of an aquatic environment where conductive heat loss is ~26 times greater than in air of a similar temperature (Rapp 1971). Otariids possess a thinner insulating hypodermal blubber layer relative to phocid seals (true seals). This is particularly true for fur seals that, true to their name, rely heavily on their pelage for insulation (Liwanağ *et al.* 2012). Fur seals, like other otariids, face additional potential thermal challenges compared to phocids because of their larger flippers, which increase their surface area to volume ratios and may serve as thermal windows (Willis *et al.* 2005).

Northern fur seals (*Callorhinus ursinus*) are relatively small (~8.5 kg) when weaned at about 4 mo of age (Baker and Fowler 1992, Gentry 1998, National Marine Fisheries Service 2007), and must contend with the frigid waters of the Bering Sea and North Pacific Ocean for 8–20 mo during their initial dispersal migration until they return to land when 1 or 2 yr old (Baker 2007). Unfortunately, due to the fact that young northern fur seals remain at sea during their postweaning months, little is known regarding their physiological development during this significant period.

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Hence, there is little information about the environmental factors that shape their distribution or affect their survival. Such information might contribute to understanding why the main breeding rookeries on the Pribilof Islands in the central Bering Sea have declined since 1998 (Towell *et al.* 2006, National Marine Fisheries Service 2007). It is particularly important to understand the interaction between water temperatures and foraging bioenergetics, given changes in oceanographic conditions and prey distribution have been identified as possible contributing factors to population declines (National Marine Fisheries Service 2007, Trites *et al.* 2007).

An endotherm's thermoneutral zone (TNZ) is defined as "the range of ambient temperature at which temperature regulation is achieved only by control of sensible heat loss, *i.e.*, without regulatory changes in metabolic heat production (H) or evaporative heat loss" (IUPS Thermal Commission 2003). In more empirical terms, it is the environmental conditions within which endotherms do not expend additional energy for cooling or heating (Schmidt-Nielsen 1997). Endotherms maintain body temperature by expending energy to cool when they are above their upper critical temperature (UCT) and to produce heat when below their lower critical temperature (LCT). The TNZ of a species is also known to differ throughout ontogeny and during specific life history events (reviewed in Nichelmann and Tzschentke 1995). Delineating an animal's TNZ is a standard measure in ecological physiology because it is assumed to define the energy requirements within certain environments as well as delineate the potential range of habitats for a species (Angilletta 2009).

Thermoneutral zones for pinnipeds have been derived from models based on the physics of conductivity and heat dynamics, and tested to various degrees with empirical data to address questions regarding marine mammal thermoregulatory limits (Hokkanen 1990, Worthy 1991, Boily 1995, Kvasdheim *et al.* 1997). While some of these models have calculated theoretical lower critical temperatures for different species (Øritsland and Ronald 1978, Watts *et al.* 1993), such simulations have not reached the point where experimental data are not required (Boily *et al.* 2000). Reported LCTs for several species of marine mammals are difficult to reconcile with known environmental conditions, particularly for younger animals. Studies have reported LCT in water of 20°C for sea otters (*Enhydra lutris*) and 14.4°C for juvenile Antarctic fur seals (*Arctocephalus gazella*), well above their usually encountered ambient water temperatures (Costa and Kooyman 1982, Rutishauser *et al.* 2004). Studies of juvenile California sea lions (*Zalophus californianus*) have found an upper critical temperature in air of 21°C–28°C (Matsuura and Whittow 1973, South *et al.* 1976), with no LCT in air as low as 10°C. However, young pups have a surprisingly high apparent LCT in air of 19°C (Thompson *et al.* 1987). While a LCT in water of 6.4°C has been reported for adult California sea lions (Liwana *et al.* 2009), the LCT in water for subadults has been reported as high as 15°C (Liao 1990).

In this study, we examined the effect of water and air temperature on the metabolic rates of young northern fur seals and attempted to define their TNZ in either medium throughout the year. The link between thermal physiology and ecology has a twofold consequence for northern fur seal conservation. Fur seals may be constrained in their ability to pursue prey into novel habitats if water temperatures limit their potential foraging ranges. Conversely, fur seals may have to expend more energy through thermoregulation (possibly compounded by additional time required to forage or travel to feeding grounds) when shifting their foraging grounds into areas where water temperatures are outside of their TNZ.

MATERIALS AND METHODS

Six female northern fur seals were transported just after weaning (~4 mo of age) from a rookery on St. Paul Island, Alaska, to the Marine Mammal Energetics and Nutrition Lab located at the Vancouver Aquarium in Vancouver, British Columbia, Canada, in October 2008. The animals were housed in seawater pools (with accompanying haul out space) with water temperatures that reflected the local ocean conditions (4°C–17°C). The animals were trained by husbandry staff from the Vancouver Aquarium, including familiarization with all research protocols and equipment.

A set of trials was conducted every 2–4 mo, during which oxygen consumption was measured while each northern fur seal was (1) dry and resting in ambient air and (2) wet and partly submerged in temperature-controlled water. Rates of oxygen consumption were measured *via* open circuit respirometry in a specially designed 340 L metabolic chamber (dimensions: 0.92 m × 0.61 m × 0.61 m). The individuals were trained to enter the chamber voluntarily under trainer control and remain calm, with minimal activity. Air was drawn through the chamber at 125 L/min using a Sable Systems 500 H mass flow generator (Sable Systems International, Las Vegas, NV) and a desiccated subsample of the excurrent airstream was analyzed for fractional concentrations of CO₂ and O₂ by Sable Systems CA-1B and FC-1B analyzers, respectively. Data was downloaded to a portable computer *via* Sable Systems' Expedata software. Changes in fractional gas concentrations were determined from baseline (ambient) measures at the start and end of each trial (which also accounted for any system drift), and the entire system was calibrated against gases of known concentrations at the start of each set of trials. Rates of oxygen consumption were calculated *via* LabAnalyst X (<http://warthog.ucr.edu/WartHogPage/LAX%20website/LAHP.html>) incorporating appropriate equations from Withers (1977).

At the start of each trial, metabolism was measured under ambient air conditions. The animals were tested in the morning at least 18 h postprandial, and were not given food during the trials. While behavior was continuously monitored, movement was minimal for most animals due to their previous training and exposure to the experimental equipment. Oxygen and carbon dioxide concentrations were recorded every second and air temperature within the chamber was recorded every 4 min. After 25 min, water was continuously pumped into the chamber from a temperature controlled reserve pool at 0, 2, 4, 6, 8, 10, or 12°C. The order of the temperature treatments was randomized within a group, but all fur seals were subject to the same order within a trial set. The chamber was filled until the animal's torso was covered (fill time ~2 min), and mechanical fail-safes prevented the water level from increasing beyond this point. The water level was sufficient to immerse the torso but prevent swimming movement. Rates of oxygen consumption were monitored for an additional 30 min (consistent with Donohue *et al.* 2000 and observed subcutaneous temperature stabilization in young fur seals; Irving *et al.* 1962), and water and air temperature within the chamber were monitored every 4 min from a digital thermometer (±0.01°C; Fisher Scientific).

Rates of oxygen consumption for animals resting in air in the dry chamber (VO₂air) and oxygen consumption while partly submerged in water (VO₂water) were calculated as the lowest average 5 min block during the last 10 min period of the specific treatment. We assumed a 30 min submergence period was sufficient to overcome most potential thermal inertia; although in reality, the metabolic rates stabilized within the first 5 min of most treatments.

Each set of trials was repeated six times as opportunities allowed: February 2009 (when 8 mo of age), April 2009 (10 mo), August 2009 (14 mo), November 2009 (17 mo), February 2010 (20 mo), and June 2010 (24 mo). Each set of trials (six fur seals at seven water temperatures) was completed within 3–4 wk. Each fur seal only completed one trial (at a single water temperature) on a given day.

Statistical analyses were completed using Prism software version 6 (Graphpad Software Inc., La Jolla, CA), with alpha set at 0.05. To test for overall changes in resting metabolism ($\text{VO}_{2\text{air}}$) between trials, we used a repeated-measures ANOVA using Geisser-Greenhouse corrections for unequal variability of differences. Tukey *post hoc* tests were used to make specific comparisons between means when overall differences were detected. As each fur seal participated in seven measurements of $\text{VO}_{2\text{air}}$ within each set of trials (one preceding each water measurement), we used a mean value of $\text{VO}_{2\text{air}}$ for each fur seal for this set of analyses.

We determined the effect of environmental (air or water) temperature on rates of oxygen separately for each set of trials. For each set of trials, we separately tested the effects of ambient air temperature when dry, ambient air temperature when wet, and water temperature on rates of oxygen consumption ($n = 7$ for each fur seal for each analysis). Specifically, we performed a segmental linear regression which identifies the best-fit intercept between two or more distinct, nonoverlapping linear regressions. The analysis identified significant inflection points in the data that would represent either upper or lower critical temperature points, and also identified data limits that contributed to the regressions using an additional Prism script. We incorporated the individual fur seal as a repeated measure, and used Prism's outlier filter to identify significant outliers (only one data point in Trial 4 was affected). Each analysis potentially yielded a lower and upper critical temperature \pm standard error for each set of trials. This analysis only reported inflection points (representing either LCTs or UCTS) if the changes in slope were statistically significant.

RESULTS

Mean metabolism (\pm SD) in ambient air across each of the six trials ranged from 232.1 ± 80.6 to 151.7 ± 46.6 mL O_2 min^{-1} (Table 1). Resting metabolic rate in ambient air during the third set of trials (summer 2009) was significantly higher than either of the first two trials, but not the later trials (overall ANOVA $P = 0.002$). As the fur seals were growing during the course of the study (particularly during the summer and fall months), there were concurrent differences in body mass between the trials. Mass-specific metabolic rates ranged from 12.5 ± 3.9 to 20.7 ± 7.0 mL O_2 min^{-1} kg^{-1} . Again, metabolism was greatest in the summer trial, but only significantly greater than the first set of trials (overall ANOVA $P = 0.006$).

Air temperatures during both the dry and wet phases of the trials also varied seasonally, with temperature highest in the mid-summer trial (Trial #3; mean = 17.8°C) and lowest in the February trials (mean temperatures Trial #1 = 4.7°C , Trial #5 = 6.5°C) (Table 1). However, the range of ambient air temperatures experienced within each of the six "dry" trials was relatively similar (Table 1). Although there is a potential effect of water temperature on air temperature during the "wet" trials, the range in air temperatures during any given set of trials were similar for either testing condition ($\sim 10^\circ\text{C}$) (Table 1). Despite this range in ambient air temperatures within the trials, there was no significant relationship between air temperature and resting metabolic rate ($\text{VO}_{2\text{air}}$) in any of the trials, such that it was not possible to delineate

Table 1. Details of the thermoregulation experimental trials with 6 northern fur seals showing ages, trial dates, mean body mass, range of air temperatures when tested in the dry chamber under dry or wet conditions, and the mean resting metabolism during the dry phase ($VO_{2\text{air}}$) of the trials as absolute and mass-specific measures (mean \pm SD). Extracted lower critical temperatures (LCT \pm SD) in water are also given.

Trial #	Trial dates (start, end)	Age (mo)	Mean mass (kg)	Air temp _{dry} range (°C)	Air temp _{wet} range (°C)	Metabolism in air (mL O ₂ min ⁻¹)	Metabolism in air (mL O ₂ min ⁻¹ kg ⁻¹)	LCT in water (°C)
1	12 February 2009 22 February 2009	8	12.17	1.5–8.8	0.8–7.8	151.7 \pm 46.6	12.5 \pm 3.9	6.8 \pm 0.9
2	31 March 2009 18 April 2009	10	9.81	2.7–16.4	4.0–15.6	153.2 \pm 51.9	15.8 \pm 5.9	8.0 \pm 1.7
3	27 July 2009 14 August 2009	14	12.47	12.3–23.9	7.2–21.3	254.4 \pm 76.9	20.7 \pm 7.0	6.2 \pm 2.9
4	2 November 2009 18 November 2009	17	14.14	4.1–12.3	3.3–9.5	232.1 \pm 80.6	16.5 \pm 5.8	3.9 \pm 1.4
5	18 February 2010 12 March 2010	20	13.16	2.9–10.2	2.3–9.4	190.7 \pm 77.5	14.6 \pm 6.3	5.4 \pm 2.7
6	26 May 2010 26 June 2010	24	14.65	10.9–20.1	6.7–16.8	211.6 \pm 73.5	14.7 \pm 5.9	6.5 \pm 1.5

either an upper (UCT) or lower critical temperature (LCT) in air over the range of testing conditions. Given the low level of variability in metabolic rates for an individual across different air temperatures, it is reasonable to conclude that the fur seals' TNZ likely extended beyond the testing conditions within any given set of trials.

LCT could be clearly defined in all six of the trials of fur seals resting in water (VO_2 water). The defined LCTs in water ranged from 3.9°C to 8.0°C (Table 1, Fig. 1). Although the defined LCT in November (3.9°C) was lower compared to the others, the error associated with the estimates precluded any statistical differences between trials. An UCT could only be defined within the tested water conditions for one of the trial periods; in November, an UCT of 8.0°C was identified (Fig. 1). Interestingly, this was the same set of trials that demonstrated the lowest apparent LCT (3.9°C).

Finally, we compared metabolism between resting metabolic rate in air (VO_2 air) and metabolism in water recorded within the defined TNZs. There were no significant differences in these two metabolic measures within any of the six trials

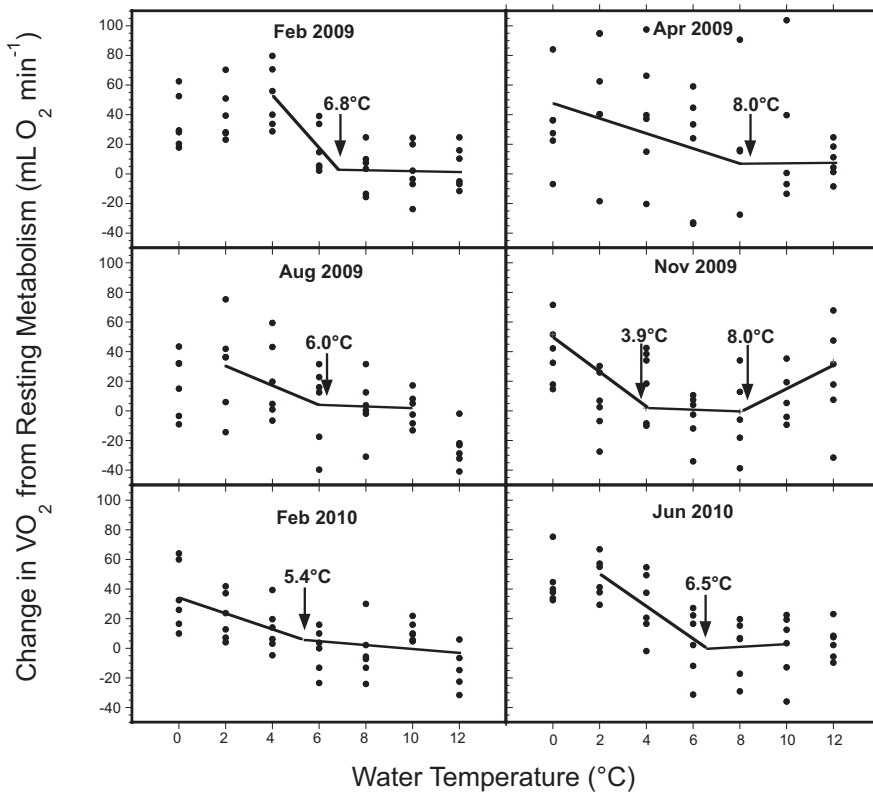


Figure 1. Changes in metabolic rates from mean values of six northern fur seals subjected to different water temperatures from February 2009 when the seals were 8 mo old, to June 2010 when they were 24 mo old. To reflect the repeated measures design, metabolism is expressed as a change in the rate of oxygen consumption from each animal's average resting metabolic rate in air within each trial set. Lower and upper critical temperatures as identified by segmented regression analysis are noted for each trial set.

($P > 0.05$), suggesting no additional heat loss within the fur seals' TNZ due to the greater potential heat conductance of water.

DISCUSSION

A number of studies contend that marine mammals have higher energy requirements than their terrestrial counterparts (Irving 1969, Pierotti and Pierotti 1983) due to the high thermal demands imposed by their aquatic (and often polar) environment (Rapp 1971), a hypothesis dismissed by Lavigne *et al.* (1986) as a byproduct of experimental error. A related hypothesis is that the distribution of marine mammals—pinnipeds in particular—is largely defined by these same thermal considerations and effectively limit the habitat of this group of animals (Trites 1990, Hansen *et al.* 1995, Angilletta 2009). One way to address the question of whether environmental conditions necessitate extraordinary energy requirements for marine mammals or limit their distribution is to measure their thermoneutral zone and compare it with their preferred or actual environmental conditions. Despite the clear importance of delineating the TNZ in pinnipeds, surprisingly few studies have defined this key eco-physiological parameter for members of this group.

Many early studies examined the effect of changes in environmental temperatures (either air or water) on physiological variables such as body temperature or skin temperature (*e.g.*, Irving *et al.* 1962, Øritsland 1968, Ray and Smith 1968, Øritsland and Ronald 1973, McGinnis 1975, Whittow *et al.* 1975). These types of measurements continue to be made, but cannot be used *per se* to define the TNZ because they are part of a marine mammal's suite of thermoregulatory adaptations, and do not necessarily incur an added energetic cost (MacArthur 1989). Likewise, behavioral changes (including posture, conspecific proximity, and microclimate selection) are not considered relevant to defining the TNZ.

Most studies that have attempted to empirically define critical temperatures in pinnipeds have been undertaken on phocid seals—particularly harbor seals (*Phoca vitulina*). Sufficient studies have been undertaken to permit some generalized predictions for other pinnipeds. Studies with young harbor seal pups indicate they have a fairly robust TNZ in air (LCT -5°C – 3°C , UCT 25°C – 31°C ; Miller and Irving 1975) that broadens slightly within the first few months and remains consistent with juvenile seals (Hansen *et al.* 1995). This trend of expansive TNZs in air is apparent among other phocid species as well, including several polar species (Ray and Smith 1968, Gallivan and Ronald 1979, Boily and Lavigne 1996). Collectively, these studies of thermal limits suggest that young phocids are usually thermally neutral within the range of normally encountered environmental air temperatures. However, the same may not be true for fur seals and other otariids.

Fur seals may be more thermally challenged than harbor seals under similar environmental conditions due to body shape and insulation differences. In our trials with northern fur seals aged 8–24 mo, no discernible lower or upper critical air temperature was detected within the range of seasonally appropriate air temperatures. The broad TNZ in air we found for our captive fur seals coincides with the results of a biophysical model that contends all natural environmental conditions experienced by northern fur seal pups on the Pribilof Islands would fall within their TNZ (Trites 1990, Trites and Antonelis 1994).

Unfortunately, there are few comparative studies published of thermoregulation in young northern fur seals. Measurements from a single young pup (3–4 mo) inferred a

lower critical temperature in air between 0°C and 6°C (Blix *et al.* 1979), while another study of slightly older pups found no metabolic response to a relatively narrow range of ambient air temperatures (approximately 19.2°C–23.5°C; Donohue *et al.* 2000). Similarly, no changes in metabolism were detected among older northern fur seals (2–5 yr) across a wider range of “environmentally relevant” air temperatures (approximately -1°C–18°C; Miller 1978; Dalton *et al.*, in press). Together, these findings suggest that air temperature may only be a concern in the youngest pups during a period they primarily remain on land, suckling.

It is interesting that some of the earliest studies of northern fur seals were concerned with the potential for overheating while on land (Hana 1924). This might seem surprising given the species’ relatively large flipper surface area (Blix *et al.* 1979) which can act as thermal windows and prevent overheating under normal activity states (Williams and Worthy 2002). Bartholomew and Wilke (1956) suggested that heat dissipation in air presented more of an issue in northern fur seals than retaining heat in cold waters due to the “burden” of their insulating pelage, going so far as to suggest that their distribution was curtailed by upper critical temperatures. A notable difference is that these authors were concerned with the ability of active animals to adequately dissipate heat in warm air environments, while measures of TNZ are performed, by definition, on inactive individuals. The consequences of overheating on land were most vividly portrayed by Ohata and Miller’s (1977) description of (often lethal) hyperthermia of 2–5-yr-old male northern fur seals that were forced to move too quickly on land during the traditional annual harvest on the Pribilof Islands (a practice now regulated).

In contrast to measurements in air, the TNZ of most phocid seals are much narrower while in water. The higher thermal challenges presented by water *vs.* air also appear to change with developmental age. Estimates of the lower critical temperature of harbor seals in water range from 12°C to 19°C for two very young animals (12–15 kg; Miller *et al.* 1976) and 20°C for slightly older harbor seals (23–33 kg, in comparison to a LCT of 2°C in air; Hart and Irving 1959), compared to 10°C for larger juvenile harbor seals (31–41 kg; Irving and Hart 1957). Surprisingly, few direct measurements have been undertaken on older harbor seals in water; however, thermodynamic models yield predictions of LCTs for adult harbor seals between -2°C and 4°C (Watts *et al.* 1993) which would conform to the general prediction of a developmental broadening in the TNZ.

As with phocids, the effect of environmental temperature on fur seal energetics should be more apparent in the water, given the increased conductivity of the medium and decreased insulation generally associated with a wetted pelage (Irving 1969). Bartholomew and Wilke (1956) stated that the “short, sparse, coarse pelage...is easily wetted and appears to be a relative inadequate insulator,” an observation reinforced by subsequent studies by Irving *et al.* (1962). The difference between thermoregulatory costs associated with dry and wet pelage was similarly demonstrated by Blix *et al.* (1979), who found that very young northern fur seal pups were able to maintain body temperature in air as cold as 0°C (partly through shivering at lower temperatures). However, body temperature of fur seals when wetted or submerged in water at 10°C or lower quickly decreased, likely as an adaptation to limit the effective thermal gradient and subsequent heat loss.

The results of our study conform to the predictions based on other pinniped studies of a narrower TNZ when immersed in water, although we would hesitate to classify fur seal pelage as “an inadequate insulator.” We found no apparent lower critical temperature under ambient air conditions, but did identify LCTs ranging from 3.9°C to

6.8°C for fur seals in water in all six of our trials. These values partially overlap with the range of lower critical temperatures in water of 6.6°C–11.1°C reported for three 7-mo-old male northern fur seals born in California (Liwanag 2010; similarly aged animals in our study had a LCT of 6.8°C). Although the current data do not permit a rigorous comparison, it would be interesting to investigate further whether there was any significant difference in thermal capacity between Bering Sea and California populations of fur seals.

We found evidence during only one of our trials of an upper critical temperature of 8°C while in water (Fig. 1). Such a relatively low temperature for a UCT was surprising, given the high heat capacity of water and the presence of arteriovenous anastomoses (specialized blood vessels) located in the flippers of otariids, which facilitate the dissipation of excess heat (Bryden and Molyneux 1978, Williams and Worthy 2002). There was no evidence of a comparable UCT in other studies of similarly aged fur seals (Donohue *et al.* 2000, Liwanag 2010), and the resulting ~4°C thermoneutral zone seems uncharacteristically narrow. This narrow UCT does not seem to relate to either resting metabolic rate or body mass. While these trials were characterized by the smallest range of testing air temperatures, as well as the lowest LCT, it is unclear how these may have contributed to defining a UCT.

Differences in the LCTs of northern fur seals in water reported in previous studies can partly be explained by developmental changes. Blix *et al.* (1979) found that very young northern fur seals were unable to maintain body temperature in water below 10°C. Similarly, Donohue *et al.* (2000) reported a possible LCT in water of between 10°C and 20°C in premolt (4–7 wk) northern fur seal pups, although their methodology and statistics did not permit a definitive identification of the LCT. This same study reported an apparent dramatic developmental effect, as (slightly older, 12–15 wk) postmolt pups appeared to be thermoneutral in water at 5°C, 10, and 20°C. This runs counter to the results of our study, as well as to a study of 7–9 mo fur seal pups that found an average LCT in water of 8.3°C (Liwanag 2010). Subsequent studies with our fur seals at older ages (2.5–3.5 yr) found no increase in metabolism across a range of water temperatures at 2°C, 10°C, and 18°C throughout the year, except for an increase in 2°C water during the summer months (Dalton *et al.*, in press). In sharp contrast to this and other studies, Miller (1978) reported a continual increase in metabolism of 2–5-yr-old northern fur seals with decreasing water temperatures between 0°C and 25°C, suggesting no thermal neutrality within this range.

Despite the overall apparent trend in increasing TNZ with physical development, we did not detect a shift in our study within the age range (8–24 mo) of our animals. This may be partly due to sample size, but it also likely reflects the limited physical growth of this species during this period (particularly for females) in contrast to other otariids, and certainly in comparison to phocid seals (Trites and Bigg 1996). Hence, if thermoregulatory capacity is largely dependent on body geometry (*i.e.*, thermal mass, surface to volume ratios), then there is little reason to expect a change in the fur seals' TNZ during this period of their lives.

Increases in thermal capacity in young fur seals may not solely be the result of changes in body size, but are also likely related to life history changes. Northern fur seals spend the majority of their first 4 mo of life on land, with only short-term excursions into local waters. Baker and Donohue (2000) suggested that the time young pups spent in the water was limited by the development of their thermoregulatory capacity. Northern fur seals do not disperse from the rookeries until they have completed their postweaning molt, after which they enter a pelagic existence. Therefore, the observation by Donohue *et al.* (2000) of a dramatic increase in thermal capacity

between pre- and postmolting northern fur seal pups suggests that this rapid change in thermal capacity is likely attributable to changes in pelage structure occurring after the first molt, rather than physiological (or body size) changes *per se*.

Ecological Impacts

Thermoneutral zones are thought to impose physiological constraints on the distribution and ecology of individuals, although a host of biological and physical features likely contribute to actual species' ranges. Northern fur seals are known for their wide-ranging dispersal across the North Pacific (Kenyon and Wilke 1953, Bigg 1990). This diaspora may be partly related to targeting reliable food resources within the productive Transition Zone Chlorophyll Front (Ream *et al.* 2005, Baker 2007), but it may also be related to thermal considerations. The dispersal from the Bering Sea in late fall is likely influenced by increasing storm frequencies towards late November (Scheffer 1950, Ragen *et al.* 1995, Lea *et al.* 2009) as well as the southward progression of sea ice, with drift ice reaching south of the Pribilof Islands from February to April (Bigg 1990, Lea *et al.* 2009). Mean air temperatures drop rapidly through October and November on the Pribilof Islands (Trites and Antonelis 1994), and mean sea surface temperatures in the Bering Sea during the time of weaning and subsequent dispersal drop from 7.4°C (October) to 5.5°C (November) (Ingraham 1983). The latter has been postulated as a cause for dispersal as well as a contributing factor to significant mass loss during their initial winter at sea (Scheffer 1981).

A study of satellite-tagged northern fur seal weanlings demonstrated that most (15 of 18) of the animals departed the Bering Sea between the end of November and the end of January (Baker 2007). Almost all animals remained above the 45°N latitude through the early spring (when the last of the tags failed), regardless of whether they had adopted a pelagic or nearshore foraging strategy. While it would be premature to conclude that the distribution of these young animals was solely due to thermal considerations, it is interesting to note that the 6°C isotherm (the "average" LCT found in this study) for sea surface temperatures reaches the Aleutian archipelago in December (when dispersal through the passes begins) and moves progressively south until its zenith in March/April at about 45°N, before progressing northwards again (Fig. 2).

A subsequent, larger study ($n = 105$) following tagged pups in November confirmed that initial dispersal date from the Pribilof Islands was closely tied to storm activity (Lea *et al.* 2009). This study also demonstrated a significant relationship between this initial dispersal movement and the intensity and direction of prevailing winds. It is difficult to ascertain the exact causal factors of this pattern given that the same climatic conditions which facilitate this potential "wind assisted dispersal" of fur seals would also affect ice coverage, sea surface temperatures, and potentially prey distribution. However, not all fur seal pups disperse out of the Bering Sea within the same time frame; some animals remain within the Bering Sea until at least January (duration of tag transmission), while others spend considerable time in proximity to the Aleutian Islands and Alaskan coast. While the exact impact of this lack of migration to warmer, more productive areas is unclear, it likely has significant bioenergetic consequences due to decreased energy intake and increased thermoregulatory costs, and may contribute to lower survival rates in this cohort. This suggests the observed increase in the frequency and intensity of storms in the North Pacific Ocean (Graham and Diaz 2001) may significantly impact postweaning survival of pups (Scheffer 1950, Lea *et al.* 2009).

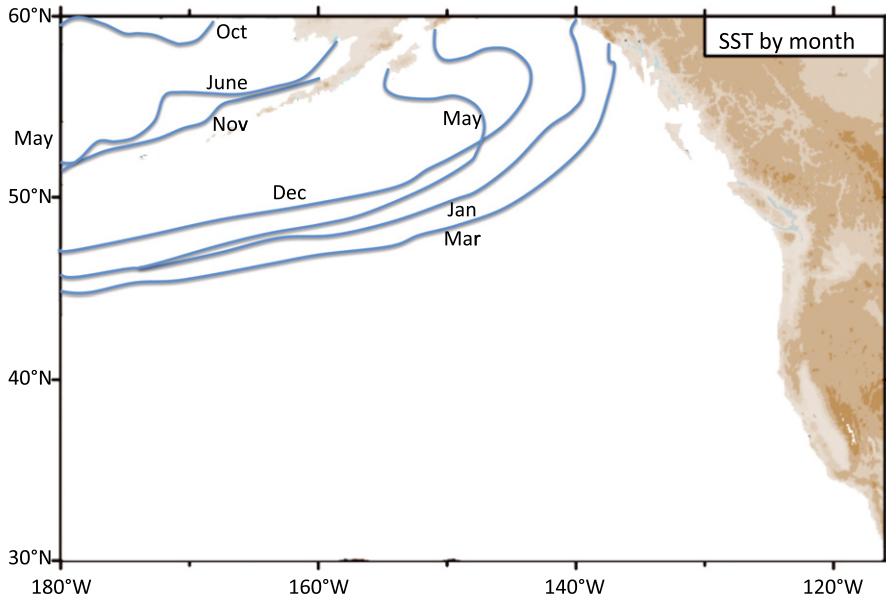


Figure 2. Monthly changes in the location of the 6°C isotherm for sea surface temperatures in the North Pacific and Bering Sea from October to June (excluding February and April for clarity). Data were derived from average monthly sea surface temperatures in the Northeast Pacific Ocean from 1982 to 2002 (Fisheries and Oceans Canada, <http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/sst-tsm/index-eng.htm>). The 6°C isotherm was chosen in reference to the average lower critical temperature of northern fur seals in water found in our study. Sea surface temperatures north of these isotherms would tend to be below the lower critical temperature, while those south of the isotherms would be within the thermal neutral zone.

Care should be taken in interpreting thermoneutral zones as strict ecological constraints (Nichelmann and Tzschentke 1995) given that LCTs can likely vary in response to seasonal thermal demands (even though we did not find any distinct seasonal trends for our fur seals). Harbor seals, for example, have been reported to alter their LCT in tandem with mean seasonal environmental temperatures (Hart and Irving 1959), which Irving (1969) suggested was a likely physiological adaptation that also acted as a constraint on population distribution (in contrast, Hansen *et al.* 1995 suggested that warm ambient temperatures restrict distribution for this species). Animals may also employ a number of alternate methods to maintain homeostasis, including those afforded by changes in microclimate selection, posture (including social proximity), behavior (Gentry 1973), alterations in defended core mass and, most relevant to marine mammals, thermal substitution from heat generated by other bioenergetic pathways (MacArthur and Campbell 1994, Kaseloo and Lovvorn 2006, Rosen *et al.* 2007, Liwanag 2010). However, fur seals may push the limits of homeostasis when seeking out submesoscale oceanographic features that tend to concentrate prey, which may include cold water eddies that incur potential thermoregulatory consequences (Nordstrom *et al.* 2012). Fur seals are also temporarily subject to colder waters at depth during foraging bouts, but these episodes are brief and likely partly mitigated by the aforementioned thermal substitution from activity and digestion.

At the broad scale, there is little doubt that thermoneutral zones represent true physiological considerations with important ecological and evolutionary consequences (Angilletta 2009). As such, the lower critical temperatures defined in our study provide insight into the possible physiological constraints of foraging ecology in young northern fur seals. Furthermore, they contribute to identifying and quantifying the energy consequences of alterations in prey distribution or ocean climate that may adversely affect fur seal populations in the wild.

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