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Spatial variation of heat flux in Steller sea lions: evidence for consistent avenues of heat exchange along the body trunk

Kate Willis[a,*], Markus Horning[a], David A.S. Rosen[b], Andrew W. Trites[b]

[a]Laboratory for Applied Biotelemetry and Biotechnology, Department of Marine Biology, Texas A&M University, 5007 Avenue U., Galveston, TX 77551, USA
[b]Marine Mammal Research Unit, University of British Columbia, 6248 Biological Sciences Road, Vancouver, BC, Canada V6T-1Z4

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Abstract

Maintaining insulative fat stores is vital for homeothermic marine mammals foraging in cold polar waters. To accomplish this, animals must balance acquisition and expenditure of energy. If this balance is shifted, body condition can decrease, challenging thermal homeostasis and further affecting energy balance. Prior studies of temperature regulation in sea lions have neither quantified basic all-inclusive heat flux values for animals swimming in cold water, nor determined whether they exhibit consistent spatial patterns of heat flux. Heat flux and skin temperature data were thus collected from four captive Steller sea lions using heat flux sensors (HFSs) with embedded thermistors. Optimal sensor placement was established using infrared thermography to locate the major areas of heat flux along the surface of the animals. Experiments were conducted on swimming animals in a large habitat tank with and without a drag harness, and on stationary animals in a temperature- and current-controlled swim flume. All heat flux measurements were corrected by a previously determined correction factor of 3.42 to account for insulative effects of the HFSs and attachment mechanism. Heat flux from shoulders and hips was consistently greater than from mid-trunk and axillary areas in both swimming and stationary animals, suggesting that certain areas of the body are preferentially used to offload excess heat. Mean heat flux for animals swimming with a drag harness was significantly greater than for unencumbered animals, indicating a likely increase in heat production beyond minimum heat loss. Thus, thermal stress does not appear to constitute significant costs for Steller sea lions swimming under conditions of increased drag at speeds of approximately 1 m/s in water temperatures of approximately 8.0 °C.

Keywords: Body trunk; *Eumetopias jubatus*; Heat flux; Spatial pattern; Thermal windows; Thermoregulation

1. Introduction

Most pinnipeds face a suite of thermoregulatory challenges resulting from their amphibious lifestyle, reproducing on land and foraging at a sea in a medium

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* Corresponding author. Tel.: +1 409 740 4541; fax: +1 409 740 5002.
E-mail address: Labb@tamug.edu (K. Willis).

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that has a conductivity 25 times greater and a specific heat 4000 times greater than that of air (Bonner, 1984; Nadel, 1984; Dejours, 1987). Phocids and odobenids meet these challenges by having considerable blubber, while fur seals and sea otters have dense pelages with water repellent underfur (Williams and Worthy, 2002). Many species of sea lion have comparatively less insulation (Costa, 1991), as they have neither deep layers of blubber nor dense mats of underfur. Most species compensate for this by inhabiting temperate or tropical climes (e.g., California sea lions *Zalophus californianus*, Australian sea lions *Neophoca cinerea*, Hooker's sea lions *Phocarctos hookeri*), where water and/or air temperatures are warmer (Perrin et al., 2002). Steller sea lions (*Eumetopias jubatus*), however, inhabit waters that can reach near-freezing temperatures (Jefferson et al., 1993).

Most early studies on thermal physiology in pinnipeds concentrated on the role of flippers as a primary site for heat transfer and temperature regulation (e.g., Bartholomew and Wilke, 1956; Irving and Hart, 1957; Hart and Irving, 1959; Irving et al., 1962; Matsuura and Whittow, 1974; McGinnis, 1975; Gallivan and Ronald, 1979), because they are poorly insulated, highly vascularized and contain vascular structures near the surface that allow for dissipation or conservation depending on thermal state of the animal (Scholander and Schevill, 1955; Tarasoff and Fisher, 1970). However, the role of heat transfer through the flippers has more recently been debated depending on whether an animal is hot or cold stressed (Watts et al., 1993; Kvadsheim et al., 1997). Øritsland (1968) suggested the importance of avenues of heat flow along the body trunk, and Kvadsheim and Folkow (1997) determined that heat flux for cold stressed phocids was minimal at the flippers and occurred predominantly through the body trunk. Recent work has supported this theory (at least for phocids) by showing extensive thermal windows on the trunks of hauled out harbor seals, harp seals and a grey seal (Mauck et al., 2003). However, these windows were neither constant in space nor time, and no study to date has directly assessed whether thermal windows or consistent spatial patterns of heat flux exist in otariids.

No direct measurements of heat flux exist for Steller sea lions swimming or feeding in water. For the Steller sea lion, incorporation of thermoregulation data into energetic models is important, since these animals inhabit regions characterized by cold air and water (Niebauer et al., 1981; Jefferson et al., 1993; Stabeno et al., 2001), and have been described as 'lean' animals with relatively thin blubber layers (Pitcher et al., 2000). Workshops have also highlighted the scarcity of physiological information for Steller sea lions, and emphasized the importance of attaining baseline information for model input (Williams et al., 1999a; DeMaster et al., 2001).

Our study quantifies heat exchange rates in Steller sea lions and presents baseline heat flux data for swimming and stationary animals. Heat flux data for animals swimming with added sources of hydrodynamic drag are also presented as a proxy for effects of increased work. Heat flux was measured at four locations on four sea lions using heat flux sensors (HFSs) following the methodology described by Willis and Horning (2004). We tested the predictions that (i) spatial patterns of heat flux obtained from HFSs for animals swimming underwater would be consistent and similar to those exhibited in air by thermal images, (ii) heat flux would be highest at areas with minimal insulation and (iii) heat flux would be greater at all locations when animals swam with additional sources of hydrodynamic drag.

2. Material and methods

2.1. Study subjects and locations

Two adult female Steller sea lions aged 9 years, identified as FKI and FSU, were used for experiments on swimming animals conducted between June and August 2002. Both animals had been captured as pups off British Columbia, and were housed in outdoor pools at the Alaska SeaLife Center (ASLC), Seward, AK, USA. Animals were fed a daily diet of walleye pollock (*Theragra chalcogramma*) and herring (*Clupea harengus*) supplemented with vitamins. Morphometrics were measured throughout the course of data collection (Table 1). Heat flux measurements were collected from animals undergoing simulated foraging sessions in a large outdoor habitat tank using the experimental setup described by Cornick and Horning (2003) and Willis and Horning (2004). Tank water temperatures ranged from 7.5 to 8.6 °C, with a mean

Table 1
Age, mass, length and girths of study animals

Animal ID	Age (years)	*n*	Body mass	Length (cm)	Girth (cm)				
					Shoulder	Axillary	Middle	Hips	Base flippers
ASLC									
FKI	9.0	3	191±4.7	220.0±2.3	n/m	141.0±1.7	128.5±4.3	92.7±1.2	n/m
FSU	9.0	2	197.3	218.3	n/m	138.3	128.5	93.0	n/m
Mean±S.D.		5	194.0±6.8	219.3±2.0	n/m	139.9±3.3	128.5±3.2	92.8±0.9	n/m
VA									
FHA	5.0	1	132.9	186.7	135.0	125.0	n/m	83.0	38.0
FSI	5.0	1	149.3	205.0	141.0	129.0	n/m	83.0	62.0
Mean		2	141.1	195.9	138.0	127.0	n/m	83.0	50.0

n/m, not measured.

of 8.1±0.3 °C. Heat flux data were also collected from Steller sea lions during a preliminary study conducted between November 2001 and February 2002 at the Vancouver Aquarium Marine Science Centre (VA), Vancouver, BC, Canada. Experiments were conducted while animals remained stationary in a temperature-regulated pool with a controlled water current (Willis, 2004), and results were used for comparison to data from swimming animals. Of the heat flux data collected on stationary animals, the data most comparable to free-swimming sea lions at the ASLC were from experiments conducted on two sub-adult female animals aged five years (Table 1), identified as FSI and FHA, tested at water temperatures of approximately 7.0 °C and flow speeds of 1.0 m/s. Animals were assumed to have acclimated after more than 30 min of immersion and heat flux data were collected using the same HFS methodology as animals at ASLC (see Willis and Horning, 2004). All experiments were conducted under Texas A&M University Laboratory Animal Care Committee AUP no. 2001-112, the ASLC's Institutional Animal Care and Use Committee AUP no. 01-001, MMPA permit no. 881-1443 and the University of British Columbia Animal Care Committee.

2.2. Heat flux and skin temperature

HFSs with integrated thermistors (Thermonetics, San Diego, CA, USA) were modified and attached to animals as described in Willis and Horning (2004). In brief, a small lip of PVC piping was glued to the rim of the HFS. Sensor holders consisting of a ring of PVC piping and circular neoprene patch were glued to the surrounding fur, pressing the sensor against a shaved patch of skin. This design permitted removal of HFSs after experimental sessions. Heat flux and skin temperature data were recorded using an animal-borne heat flux recorder (HFR) measuring 13×5×2 cm, developed by M. Horning, capable of recording data from four heat flux and thermistor sensor pairs. HFS output was converted to heat flux data using calibration constants provided by the manufacturer. Temperature dependent correction factors were calculated from sensor data recorded during thermistor calibrations in a temperature controlled circulating water bath (Willis and Horning, 2004). Constant offsets were added when values from balanced sensors in air differed from zero by similar amounts before and after each session. Effects due to the thermal resistance of HFSs and the attachment mechanism were assessed as described in Willis and Horning (2004). Combined effects were insulative and consistent across water temperatures and flow speeds, resulting in a correction factor of 3.42 times measured heat flux (Willis and Horning, 2004).

2.3. Swim speed

A swim speed recorder (SSR) as described in Horning and Trillmich (1997) was used to measure the speed at which animals swam over a range of 0.25–6 m/s at a resolution of 0.05 m/s. This device sampled water flow from a frontal inlet through an impeller to a top-mounted outlet. Data were sampled at a rate of one per second and downloaded via a custom interface after each recording session.

2.4. Infrared thermography

To assess differences in heat flux across the surface of animals, an a priori decision was made to place two HFSs on areas of high and low heat flux, respectively, called 'hot spots' and 'cold spots'. Optimal spot locations were determined using infrared thermography to identify major areas of heat flux from the surface of the study animals. Infrared thermography has been applied to biological and physiological studies on birds (Hill et al., 1980; Best, 1981; Phillips and Sanborn, 1994; McCafferty et al., 1998), reptiles (in den bosch, 1983; Blumberg et al., 2002), insects (Cena and Clark, 1972), marine mammals (Liao, 1990; Cuyler et al., 1992; Dehnhardt et al., 1998; Williams et al., 1999b; Mauck et al., 2000; Pabst et al., 2001; Meagher et al., 2002; Mauck et al., 2003) and terrestrial mammals (Cena and Clark, 1973; Korhonen and Harri, 1986; Mohler and Heath, 1988; Lancaster et al., 1997). Thermal images were taken of Steller sea lions at the ASLC using a FLIR Systems ThermaCAM® PM 695 thermal imaging camera (FLIR Systems, Boston, MA, USA). This system has a thermal sensitivity of 0.08 °C at 30 °C and a field of view/minimum focus distance of 24×18°/0.3 m. Spatial resolution is 1.3 mrad, and image frequency is 50/60 Hz non-interlaced, producing a TV-like real-time thermal image that was not affected by animal movement. Images were taken of two adult females during 10 separate outdoor photography sessions for no longer than 5 min immediately after emergence from water of ambient temperature (mean=8.1 °C; range=7.5–8.6 °C). Images were thus always taken when animals were wet and motionless in one of two postures (lying on a rock or 'standing' on hind flippers and leaning up against a rock). Between 21 and 42 images were taken per session, and these images were stored digitally and analyzed using customized image analysis software (ThermaCAM™ Researcher 2001, FLIR Systems). All images were analyzed using a 'rainbow' color scheme (Dehnhardt et al., 1998) and were screened for consistent hot and cold spots. For each image, surface temperatures were calculated for eight distinct areas that exhibited consistent thermal behavior throughout all sessions. These were labeled according to their location on the animal, e.g., nose, eyes, dorsal posterior foreflipper base (DPFB), hips, shoulders, middle girth and axillary girth.

2.5. Ultrasonic imaging of blubber thickness

For animals at the ASLC, blubber thickness and skin depths were measured at the four HFS locations using a Sonosite Portable Ultrasound Imaging System, Sonosite 180 VET plus C60 abdominal transducer unit (Sonosite, Bothell, WA, USA) as described in Mellish et al. (2004).

2.6. Experimental design

Equipment was attached as detailed in Willis and Horning (2004). In brief, a 13×5×2 cm baseplate for the detachable HFR/SSR unit was attached to the sea lion's dorsal fur with 10-min epoxy. Four HFS holders were attached using Loctite QuickTite® cyanoacrylate gel to fur surrounding a shaved patch. Each experimental session consisted of placing the HFR/SSR combination and HFSs into their baseplate and sensor holders while the animal remained under behavioral control. The session commenced when the animal entered the water. Swim speed, heat flux and skin temperature measurements were collected from each animal as they swam in water temperatures ambient to Resurrection Bay, Alaska (mean=8.1±0.3 °C; range=7.5–8.6 °C). Additional measurements of swim speed, heat flux and skin temperature were collected from animal FSU while she wore a drag-increasing harness for a separate study. The harness was constructed of nylon webbing with plastic frills estimated to increase hydrodynamic drag by between 10% and 15% (L. Cornick, personal communication). During trials ranging from 4 to 9 min, animals swam between a foraging setup consisting of a series of subsurface feeding tubes (see Cornick and Horning, 2003). When all fish had been released and consumed (between 2.0 and 5.0 kg), the trial ended with the animal surfacing after the last dive, and the HFR and HFSs were removed from the animal. Exclusion criteria as detailed in Willis and Horning (2004) were applied to all data sets.

Previous studies on pinniped energetics and thermoregulation have used acclimation times between 0 and 3 hours in water (Irving and Hart, 1957; Feldkamp, 1987; Folkow and Blix, 1989; Rosen and Trites, 1997; Donohue et al., 2000; Noren, 2002; Rosen and Trites, 2002), and between 1 and 5 h in air (Whittow et al., 1972; Folkow and Blix, 1989; Hansen et al., 1995; Boily and Lavigne, 1996; Hansen and Lavigne, 1997; Kvadsheim and Folkow, 1997; Boily et al., 2000). In our study, animals were removed from their habitat and held in tanks of comparable water temperatures for up to 20 min while the foraging setup was assembled, resulting in the sea lion spending minimal time out of the water prior to experiments. Animals were therefore assumed to have acclimated to water temperatures in the habitat area.

2.7. Statistical analyses

For each experimental session, total session duration was calculated, and mean values for heat flux and skin temperature, along with standard deviations were computed. All data were analyzed using UMVIEW data analysis software (Mohren and Horning, 1996), and SPSS 10.0 for Windows (SPSS, 1999). Least-squares linear regressions were used when indicated. Repeated-measures ANOVAs were used to account for the non-independence of spatial data. Friedman repeated measures on ranks was employed for repeated-measures distributions with unequal variances. When significant, Tukey's multiple pairwise comparisons or Tukey's multiple pairwise comparisons for ranked data were performed. All data were explored for sphericity, normality and equality of variances where appropriate using Mauchley's, Kolmogorov–Smirnov and Levene's tests, respectively. For non-normal distributions or those with unequal variances, Mann–Whitney rank sum and Wilcoxon signed ranks tests were used where indicated. All means are arithmetic means and are presented with ±S.D. or S.E.M where appropriate. Results were deemed significant at $p<0.05$, unless otherwise noted.

3. Results

3.1. Morphological and ultrasound data

Morphological and ultrasound data are summarized in Tables 1 and 2. There were no significant differences between body masses for animals FKI (191.8±4.7 kg) and FSU (197.3±10.3 kg) (Mann–Whitney test, $n_1=3$, $n_2=2$, $p=0.56$). For both animals, blubber and skin thickness at the middle and axillary girths were greater than those at the hips and shoulders, but these differences were not tested for significance due to a sample size of two animals. Heat flux decreased with increasing mean blubber thickness at each of the attachment points both individually for animal FKI (least-squares linear regression, $y=3852.1-1856.0x$, $r^2=0.55$, $F_{1,2}=2.5$, $p=0.26$; Fig. 1) and animal FSU (least-squares linear regression, $y=7118.8-3411.7x$, $r^2=0.65$, $F_{1,2}=3.7$, $p=0.19$; Fig. 1), and for both animals combined (least-squares linear regression, $y=3234.2-1382.3x$, $r^2=0.43$, $F_{1,6}=4.5$, $p=0.08$; Fig. 1); however, these relationships were not significant.

3.2. Infrared thermography

Infrared temperature readings indicated the nose, eyes, DPFB, hips and shoulders as potential hot spots (Fig. 2; Table 3). Lateral locations along the middle and axillary girth lines appeared to be cold spots (Fig. 2; Table 3). HFSs were not placed on the nose, eyes, DPFB or flippers because of difficulties associated with adequate attachment to those locations. A Friedman repeated-measures ANOVA tested for differences in temperature readings between locations at the hips, shoulders, and lateral locations along the middle and

Table 2
Blubber and skin thickness of study animals

Animal ID	Hips		Middle girth		Axillary girth		Shoulders	
	Blubber (cm)	Skin (cm)	Blubber (cm)	Skin (cm)	Blubber (cm)	Skin (cm)	Blubber (cm)	Skin (cm)
FKI	1.47	0.43	1.76	0.54	1.73	0.40	1.29	0.32
FSU	1.74	0.27	1.97	0.43	1.93	0.34	1.80	0.21
Mean	1.61	0.35	1.87	0.49	1.83	0.37	1.55	0.27

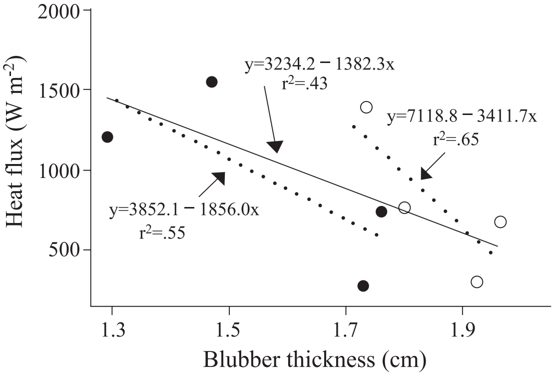

Fig. 1. Heat flux as a function of blubber thickness measured using ultrasound at all locations where HFSs were placed for animals FKI (closed circles) and FSU (open circles). Each point represents one blubber thickness measurement at a given location. Least-squares linear regressions and accompanying equations are for individual animals (dotted lines) and both animals combined (solid line).

Table 3
Skin temperature measurements and resulting HFS placement from thermal images

Location	*n*	Location type	Skin temperature± S.E.M. (°C)
HFS			
Middle girth	75	cold spot	8.6±0.1
Axillary girth	75	cold spot	8.6±0.1
Shoulders	75	hot spot	9.4±0.1
Hips	75	hot spot	9.7±0.1
Others			
Flippers	99	cold spot	7.5±0.1
DPFB	68	hot spot	10.4±0.1
Eyes	48	hot spot	15.8±0.3
Nose	24	hot spot	17.8±0.5

DPFB, dorsal posterior foreflipper base.

axillary girth lines. The effects of location were significant (Friedman repeated-measures ANOVA on ranks, χ^2_3=185.5, p<0.0001), and skin temperature values from the shoulders and hips were significantly higher than lateral locations along the middle and axillary girth lines (Tukey multiple pairwise comparison for ranked data, p<0.05). HFSs were therefore placed on lateral locations along the axillary and middle girth lines for representative cold spots, and on the shoulders and hips for representative hot spots for all subsequent data collection.

3.3. Spatial variation in heat flux

Heat flux and skin temperature data were collected throughout 7 and 11 separate experimental sessions for animals FKI and FSU, respectively. Five of the 11 sessions for animal FSU included sessions with an attached drag harness and are described below. Session durations ranged from 3 min, 54 s to 8 min,

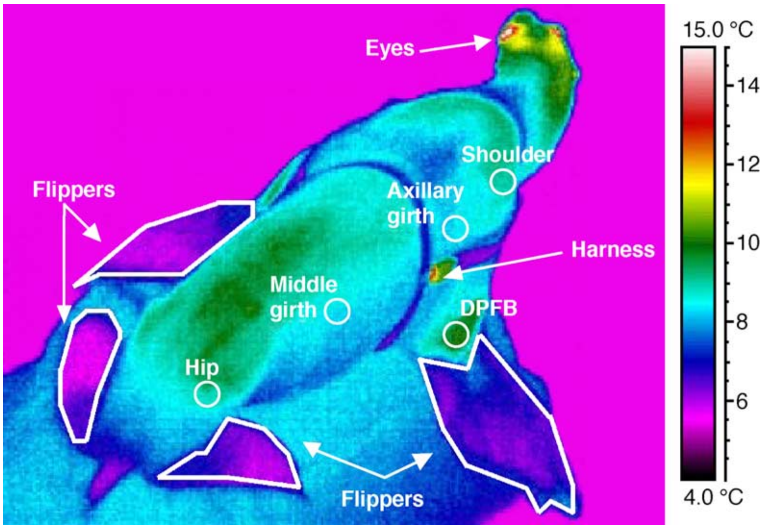

Fig. 2. Thermal image example with areas of skin temperature measurements marked according to location along the surface of the animal. Black and purple indicate coldest temperatures and red and white indicate hottest temperatures. White lines bound areas used in temperature calculations for hind- and foreflippers. DPFB, dorsal posterior foreflipper base.

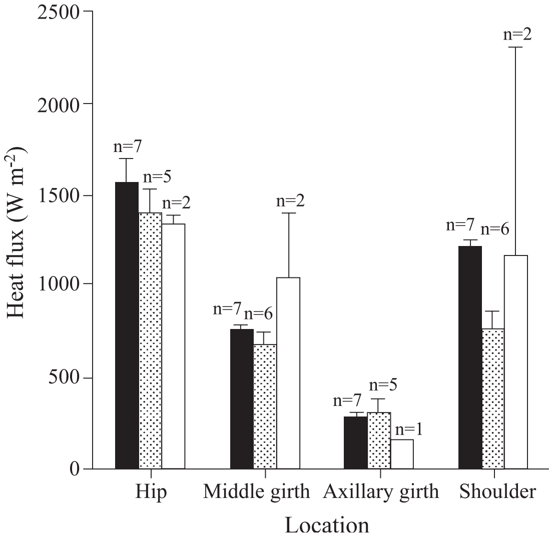

Fig. 3. Spatial differences in heat flux between four locations. Mean heat flux±S.E.M. from swimming animals FKI and FSU are shown in solid black and dotted bars, respectively. Mean heat flux±S.E.M. for stationary animals at the VA are shown in white bars.

52 s. Data were excluded from the hip and axillary girth locations during one experimental session for animal FSU when sensors fell out of their holders. For both animals, heat flux was higher in the hips and shoulders than in the middle and axillary girths (Fig. 3). These results were consistent with results from thermal image analyses in which areas along the hips and shoulders were designated hot spots and areas along the middle and axillary girths were designated cold spots. Mean heat flux values between animals FKI and FSU were different depending on location (two-way repeated-measures ANOVA, $F_{3,33}$=5.76, p=0.04), with much higher values for shoulders in animal FKI (Fig. 3). Heat flux data were therefore analyzed separately for each animal. For animal FKI, there were significant differences in heat flux between locations (Friedman repeated-measures ANOVA, χ_3^2=20.0, p=0.000) (Fig. 3). Mean heat flux was significantly higher at the hips and shoulders than the axillary and middle girths, which did not differ from each other (Tukey's multiple pairwise comparisons for ranked data, p<0.05). For animal FSU, there were also significant differences in heat flux between locations (repeated-measures ANOVA, $F_{3,15}$=64.4, p=0.000) (Fig. 3). Mean heat flux was highest at the hips, lowest at the axillary girth, and intermediate at the middle girth and shoulders, which did not differ from each other (Tukey's multiple pairwise comparisons, p<0.05). In stationary animals at the VA, mean heat flux at the hips and shoulders was higher than at the middle and axillary girths (Fig. 3).

The magnitude of heat flux measurements from the present study were, on average, an order of magnitude greater than values obtained from previous research that used HFSs on pinnipeds (Willis and Horning, 2004). Only four published studies have reported heat flux values obtained using HFSs on pinnipeds (Ohata and Whittow, 1974; McGinnis, 1975; Blix et al., 1979; Kvadsheim and Folkow, 1997), and values vary considerably across species (range: 10.0–647.3 W m^{-2}), the medium and temperature in which measurements were made, body mass, and the location of HFS placement (see Table 2 in Willis and Horning, 2004). Most of these data were collected on pups, and none of these studies measured heat flux at specifically determined hot spots. Only Kvadsheim and Folkow (1997) corrected for the thermal resistance of HFSs. It is therefore likely that the differences in magnitude between heat flux measurements from past studies and those from the present study are due to our incorporation of a thermal resistance and attachment mechanism correction factor of 3.42 times measured heat flux, combined with measurements from verified hot spots (see discussion in Willis and Horning, 2004).

3.4. Effects of increased hydrodynamic drag

Mean heat flux was 86% higher in sessions with drag than non-drag for animal FSU (Wilcoxon signed ranks test, Z=−3.7, n_1=20, n_2=22, p=0.001; Table 4),

Table 4
Difference in swim speed, heat flux and skin temperature between drag and non-drag sessions

Measurement	Drag	Non-drag	P
Session duration (m:ss)±S.E.M.	5:37±0:34 (5)	6:00±1:43 (6)	0.99
Swim speed (m s^{-1})±S.E.M.	1.0±0.00 (5)	1.3±0.01 (6)	0.004
Heat flux (W m^{-2})±S.E.M.	1449.0±140.4 (20)	779.9±93.1 (22)	0.001
Skin temperature (°C)±S.E.M.	9.3±0.1 (20)	8.6±0.1 (22)	0.0005

Heat flux values are means from all locations.
Numbers in parentheses represent number of means.

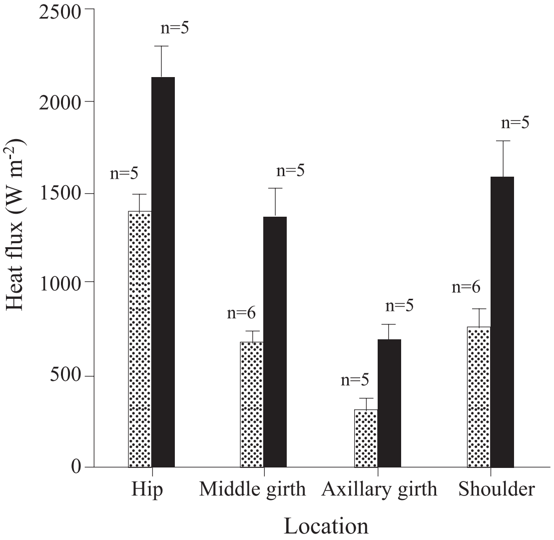

Fig. 4. Effects of increased hydrodynamic drag on heat flux plotted by location of HFS placement for animal FSU. Mean heat flux±S.E.M. from sessions with and without an added drag harness are shown in solid black and dotted bars, respectively.

and increased at all locations when the animal wore the drag harness (Fig. 4). Mean skin temperature was also higher in sessions with drag than non-drag (Wilcoxon signed ranks test, $Z=-3.5$, $n_1=20$, $n_2=22$, $p=0.0005$; Table 4). There was no significant interaction between the presence of the drag harness and specific locations (repeated-measures ANOVA, $F_{3,9}=3.0$, $p=0.06$), indicating that effects of drag were consistent across all locations (Fig. 4). Mean swim speed was slower in sessions with drag than non-drag (Mann–Whitney test, $U=0.00$, $n_1=5$, $n_2=6$, $p=0.005$; Table 4), and there was no difference in mean session duration for trials with and without drag (Mann–Whitney test, $U=15.0$, $n_1=5$, $n_2=6$, $p=0.99$; Table 4).

4. Discussion

In Steller sea lions, patterns of heat loss seen in thermal images were consistent with direct measurements of heat flux using HFSs. Thermal images taken after animals emerged from ~8.0 °C water (Fig. 2) showed temperatures were highest at the nose, eyes, DPFB, hips and shoulders, and were lowest at the flippers, middle and axillary girths (Table 3). Results from HFS analyses were concordant with these images and showed consistent spatial patterns along the bodies of swimming and stationary animals (Fig. 3). These results demonstrate that areas around the hips and shoulders are consistent avenues for heat loss in Steller sea lions. Such patterns can be explained in terms of underlying insulation, physiological adjustments in heat transport within the body, including perfusion near the surface, and heat generation due to muscular activity.

Blubber thickness varied between animals and according to location (Table 2). Although heat flux decreased with increasing blubber thickness (Fig. 1), the relationship was not statistically significant. This may have been due to small sample sizes and large inter-individual variability, as only one ultrasound measurement was made per location on each animal. However, the most poorly insulated areas along the body trunk (the hips and shoulders) clearly exhibited higher heat flux when compared to areas with greater insulation (the middle and axillary girths) (Fig. 3). Effects of insulation also help to explain differences in heat flux observed between both animals (Fig. 3). Blubber thickness was thinner for animal FKI than FSU at all but one location (Table 2), and heat flux was almost always higher in the former. Also, the largest disparity in insulation between both animals was found at the shoulders, where blubber was 1.4 times thicker for animal FSU than FKI.

Interacting effects of exercise and cold water, where animals generate additional heat from muscular work while also trying to minimize heat loss to the surrounding water, were also likely factors in resultant patterns of heat flux. Homeothermic animals respond to cold water by increased insulation and peripheral vasoconstriction, whereby the thermal gradient between core and ambient temperature is widened and insulation increases (Spotila and Gates, 1975; Schmidt-Nielsen, 1997; Pabst et al., 1999). However, this relationship is extremely complicated (MacArthur, 1989), as the contribution of exercise to thermoregulation in water involves a complex network of interactions between insulation, body mass, peripheral blood flow, exercise level, behavior and water temperature (Williams, 1986; MacArthur, 1989; Noren et al., 1999; Williams et al., 1999b). For example, the extremities could exhibit higher levels of heat loss either due to inadequate insulation or by dumping excess heat generated by locomotion, as has been exhibited in some studies on swimming marine mammals (Hampton and Whittow, 1976; Gallivan and Ronald, 1979; Noren et al., 1999; Williams et al., 1999b). For animals in the present study, the higher values of heat flux exhibited around the hips and shoulders support the latter scenario, as those locations were closest to areas associated with the highest muscle activity for swimming otariids (Howell, 1930; Reed et al., 1994). However, although no thermal neutral zone (TNZ) determinations have been conducted for Steller sea lions, water temperatures at the ASLC (7.5–8.6 °C) were much lower than the lower critical temperature (T_{lc}) of approximately 14.0 °C reported for California sea lions (*Z. californianus*) (Liao, 1990). Additionally, sea lions in our study consumed food during trials. In some mammals, the heat increment of feeding (HIF) resulting from both mechanical and biochemical processes of digestion has been demonstrated to offset thermoregulatory costs (Masman et al., 1988; Chappell et al., 1997). However, this has also been shown not to occur among other mammals (Klassen et al., 1989; MacArthur and Campbell, 1994), including Steller sea lions (Rosen and Trites, 2003).

To further explore the theoretical contribution of heat generated by locomotion to animals swimming in cold water and potential effects of HIF, results from swimming animals at the ASLC were compared to heat flux data collected from stationary animals at the VA. The spatial pattern observed in swimming animals, with highest heat flux at the hips and shoulders, was also apparent in stationary animals (Fig. 3). Keeping the significant constraints of sample size and differing animal ages, sizes and blubber thickness in mind, the magnitude of heat flux values obtained from stationary animals was similar to values in swimming animals (Fig. 3). This suggests that heat generated by locomotion and the heat increment of feeding in swimming animals did not create additional heat that needed to be dumped in order to maintain thermal homeostasis. We therefore speculate that swimming animals at the ASLC were swimming under conditions where—even if outside of their TNZ—heat loss was more or less balanced by heat produced through locomotion and other non-obligatory processes. Observed spatial patterns of heat flux were thus less likely the result of heat generated through muscular activity than the result of insulation and adjustments in perfusion.

Only when the workload increased due to added sources of hydrodynamic drag, did the amount of heat transferred change. Heat flux increased by between 53% and 125% depending on location, with a mean increase of 86% at all locations combined for animal FSU swimming with added drag (Fig. 4). Skin temperatures were also significantly higher, and the animal swam significantly slower (Table 4), showing that the observed increase in heat flux was not merely due to changes in water flow, but was related to increases in metabolic heat production resulting from increased work. It is conceivable that the drag harness produced secondary effects such as increased peripheral perfusion resulting from increases in stroke frequency due to increased locomotor effort. Although stroke frequency was not measured in the present study, in Weddell seals, the number of strokes executed is linearly related to oxygen consumption (Williams et al., 2004). Although it is not known whether this same relationship exists in Steller sea lions, based on the findings from Williams et al. (2004), we speculate that if there were increases in peripheral blood flow in animals from the present study due to changes in swimming mechanics with increases in drag, they were likely tied to increases in metabolic rate. Since mean session durations between trials with and without drag did not differ (Table 4), the observed differences in heat flux were not due to longer or shorter session times. In addition, the magnitude of increases did not differ between locations, further supporting the hypothesis that locations along the hips and shoulders represent optimal thermal windows for heat dissipation, regardless of swimming effort. These findings suggest that animal FSU was not cold stressed when wearing the harness, and that the heat produced by swimming with drag was likely enough to cover obligatory thermal costs.

Although our results do not allow us to conclusively determine whether a swimming sea lion without drag would also be able to cover such costs, they do provide insight into the thermal state of a swimming animal and the effects of increased work. The amount of work that an animal must expend to move through water is a function of its velocity, as drag increases exponentially with increases in speed

(Feldkamp, 1987; Fish, 1992, 1993; Hind and Gurney, 1997; Costa and Williams, 1999). This is especially important for animals foraging at sea, as the energetic costs of swimming and foraging are critical components to their overall energy budgets (Williams, 1999; Williams et al., 2000; Rosen and Trites, 2002). Nutritional stress is hypothesized to have been a leading cause for the initial population decline of Steller sea lions (Merrick et al., 1987, 1997; DeMaster et al., 2001; Trites and Donnelly, 2003). The amount of time spent searching for food and resulting energetic repercussions are thus significant, since higher energetic costs are thought to result from increased levels of surface swimming, often indicated by greater distances traveled while at sea (Arnould et al., 1996; Costa et al., 2000). Therefore, if increased time spent looking for food is comparable to increased work, and if this work is analogous to that produced by the drag harness (exhibited as increases in heat flux), we speculate that thermal stress is not likely to constitute significant costs for foraging Steller sea lions swimming at speeds of 1.3 m/s and at mean water temperatures of 8.1±0.3 °C.

5. Conclusions

The thermal images and results from HFSs suggest that specific areas along the body trunk are consistent avenues for heat exchange in both swimming and stationary Steller sea lions. These patterns of heat loss are likely related to underlying layers of insulation, along with physiological adjustments in heat transport. Using HFSs to collect data from free-swimming animals provides a unique opportunity to assess spatial heat flow patterns at higher resolutions and under conditions that were previously impossible. The results we report here need to be seen within the context of the very large effect of the HFSs and sensors holders, even though this effect was corrected for. Indeed, the magnitude of heat flux values obtained for Steller sea lions in the present study was much higher than values reported for other pinniped species. However, most of these reported values were collected from pups and without prior identification of hot spots. The heat flux values we report here for cold spots convert to metabolic rates within the published rates for Steller sea lions (see Willis and Horning, 2004). Thus, the value of the approach utilized here lies in the ability to collect heat flux data with one and the same methodology under different environmental and behavioral conditions that can then be compared both within and among pinniped species. Further data collection could provide additional insights into the foraging energetics of wild animals, while also providing more baseline information for bioenergetic model input.

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