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A novel approach to measuring heat flux in swimming animals

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Abstract

We present a design for long-term or removable attachment of heat flux sensors (HFSs) to stationary or swimming animals in water that enables collection of heat flux data on both captive and free-ranging pinnipeds. HFSs were modified to allow for independent, continuous, and long-term or removable attachment to study animals. The design was tested for effects of HFSs and the attachment mechanism on resultant heat flux. Effects were insulative and consistent across water temperatures and flow speeds, resulting in a correction factor of 3.42. This correction factor was applied to all measurements of heat flux from animal experiments to account for the thermal resistance of HFSs and insulative effects of the attachment mechanism. Heat flux and skin temperature data were collected from two captive Steller sea lions (*Eumetopias jubatus*) as they swam in a large habitat tank over time periods ranging from approximately 4 to 9 min. Of the 72 HFSs deployed using the attachment mechanism, data were successfully retrieved from 70. The HFS attachment mechanism was also used on two wild free-ranging Weddell seals (*Leptonychotes weddelli*) off Ross Island, Antarctica, for up to 7 days. Heat flux data were retrieved from all eight sensors deployed. These results, along with those from Steller sea lions, suggest that HFSs can be deployed with success on captive and wild animals using the designed attachment mechanism.

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1. Introduction

Aquatic homeotherms of the order Pinnipedia (seals, sea lions, fur seals, and walruses) must maintain a constant body temperature of approxi-

mately 37 °C by balancing heat loss with metabolic heat production, which can significantly affect their overall energy budget. Heat retention is facilitated by insulating layers of blubber or fur, countercurrent heat exchangers (Scholander and Schevill, 1955; Pabst et al., 1999; Williams and Worthy, 2002), and through surface area to volume ratios that are approximately 23% smaller than those of terrestrial mammals of comparable size (Innes et al., 1990). To dissipate heat, these insulative adaptations are bypassed. In furred

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pinnipeds, this occurs at thinly covered areas where heat is lost via conduction or convection from exposed body surfaces (Bartholomew and Wilke, 1956; Irving et al., 1962; Pabst et al., 1999). Heat can also be lost through other poorly insulated areas, such as flippers (Irving and Hart, 1957; Tarasoff and Fisher, 1970), or by circumventing countercurrent heat exchangers and shunting blood flow directly to the skin surface (Scholander and Schevill, 1955; Kvadsheim and Folkow, 1997; Pabst et al., 1999; Williams and Worthy, 2002). Behavioral responses, such as entering water or increasing exposed surface areas, also help dissipate heat (Bartholomew and Wilke, 1956; Whittow et al., 1971; Gentry, 1973; Williams and Worthy, 2002).

Prior studies have used a suite of techniques to estimate heat exchange including estimates based on metabolic rates (e.g., Gallivan and Ronald, 1979; Thompson et al., 1987; Hansen et al., 1995; Boily and Lavigne, 1996; Hansen and Lavigne, 1997; Donohue et al., 2000), theoretical calculations using skin, core, and ambient temperature measurements (e.g., Hansen et al., 1995; Kvadsheim et al., 1996; Hansen and Lavigne, 1997; Boily et al., 2000; Boyd, 2000; Noren, 2002), and thermal image analysis (e.g., Liao, 1990; Mauck et al., 2003). However, limitations exist with these techniques; metabolic rate can only be roughly estimated as field metabolic rate using doubly labeled water or through respirometry on animals that are not free ranging. Theoretical calculations of heat flux in water entail calculating conductive and convective heat losses (e.g., Hokkanen, 1990; Watts et al., 1993; Boily, 1995), and such equations require input of various constant and measured parameters (see Leyton, 1975; Mitchell, 1976; Campbell, 1977). For an animal in water, required skin temperature values can be difficult to collect since an accurate calculation of heat flux requires a true value for skin temperature which cannot be obtained unless a thermistor is embedded just below the surface of the skin (e.g., Folkow and Blix, 1989; Kvadsheim and Folkow, 1997; Boily et al., 2000). Finally, thermal imaging systems cannot be used underwater, thus, heat exchange can only be estimated from animals in air.

Heat exchange can be measured directly via heat flux sensors (HFSs), resulting in expressions of heat exchange between an animal's body and its environ-

ment in terms of heat flux in units of energy transferred per unit area (W m^{-2} ; Bligh and Johnson, 1973). HFSs produce an output voltage that is directly proportional to thermal flux and have been used successfully in a number of studies quantifying heat exchanges in marine mammals (e.g., Ohata and Whittow, 1974; McGinnis, 1975; Blix et al., 1979; Kvadsheim and Folkow, 1997; Noren et al., 1999; Williams, 1999b; Williams et al., 1999; Meagher et al., 2002). However, mechanisms for long-term attachment in water have traditionally been difficult to develop, thus preventing the acquisition of heat flux measurements on animals independent of direct human assistance. Of the studies that have measured heat flux directly, few exist for otariids, and just one has been conducted on Steller sea lions, albeit only in air (Williams, 1999b). To date, no direct measurements of heat flux have been obtained from swimming pinnipeds.

Several studies have used HFSs to measure heat flux in stationary marine mammals, but few have attempted to test for the effects of the sensors themselves on the measurements made (e.g., McGinnis and Ingram, 1974; Kvadsheim and Folkow, 1997). Errors in heat flux estimates are high if the HFS is placed over material of lower thermal resistance (R) ($^{\circ}\text{C m}^2 \text{W}^{-1}$) than the HFS itself (R_s) (Ducharme et al., 1990). However, if R_s is small compared to the thermal resistance of underlying material like skin and blubber, then errors due to the application of the HFS should be negligible, especially when compared to the effects of attachment devices, such as sensor holders (Wissler and Ketch, 1982; Ducharme et al., 1990). Any mounting system used to hold HFSs in place could create insulative or dissipative effects, whereby the attachment mechanism insulates areas around the HFS or increases fluid movement, respectively.

Here, we present an easily replicable design that enables long-term or removable attachment of HFSs to stationary or swimming animals in water suitable for collecting data from captive and free-ranging pinnipeds. Design requirements included (1) devising a low-impact attachment mechanism that ensured reliable contact between the HFS and shaved skin surface without placing glue directly on the bare skin of the animal; (2) designing a removable attachment mechanism appropriate for short-term work with captive animals to minimize occurrence of biting or

chewing at the HFSs; and (3) designing a comparable long-term attachment mechanism suitable for free-ranging animals. After developing a design meeting these requirements, we tested for effects of HFSs and the attachment mechanism on resultant heat flux measurements.

2. Materials and methods

2.1. Instrumentation

2.1.1. Heat flux sensors

HFSs comprised of miniature serial thermopiles (Thermonetics, San Diego, CA, USA) were used to quantify thermal energy transfers between study animals and the surrounding environment (Fig. 1). HFSs were flat, waterproofed disks measuring 2.9×0.2 cm. A thermistor implanted onto the surface of the sensors measured skin temperature (Fig. 1A).

The sensitivity of HFSs was listed by the manufacturer as 0.01 W m^{-2} . All HFSs were modified to allow for independent and long-term or removable attachment to the study animals. A 3.3×0.5 cm ring of PVC piping was glued to the silicone edge of the sensor with silicone adhesive to secure the sensor to custom-made holders (Fig. 1B). Sensor wires were terminated in a wet pluggable connector (Impulse Enterprises, San Diego, CA, USA) to fit input ports of the heat flux recorder (described below). Nylon sheathing was stretched over the length of the sensor cable for protection and attached to both the sensor and the connector ends using silicone adhesive (GE Silicone II, Huntersville, NC, USA) and ANCOR Marine Grade™ adhesive-lined heat-shrink tubing (Fig. 1C).

Sensor holders (Fig. 2) were constructed using a 4.2×0.8 -cm piece of lipped PVC (Fig. 2A,B) glued with Loctite QuickTite® cyanoacrylate gel to circular patches of neoprene (Fig. 2C) measuring 9.5-cm

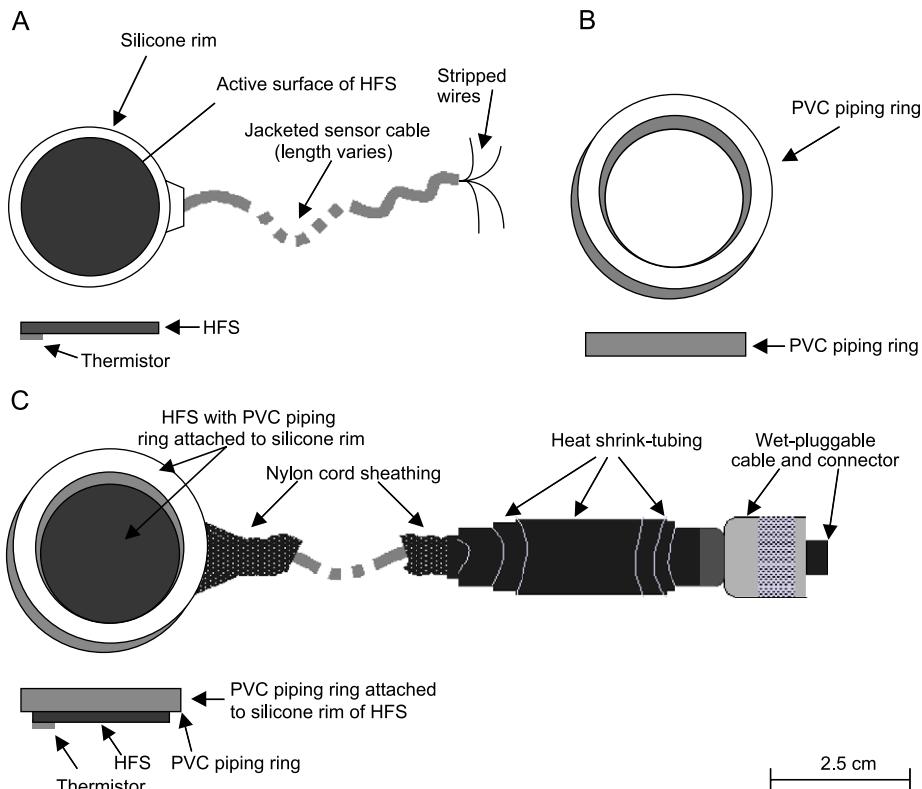


Fig. 1. Heat flux sensors (HFSs) as received from the manufacturer (A), PVC piping modification (B), and modified HFS with connector attached (C). All diagrams show top (above) and corresponding side views (below).

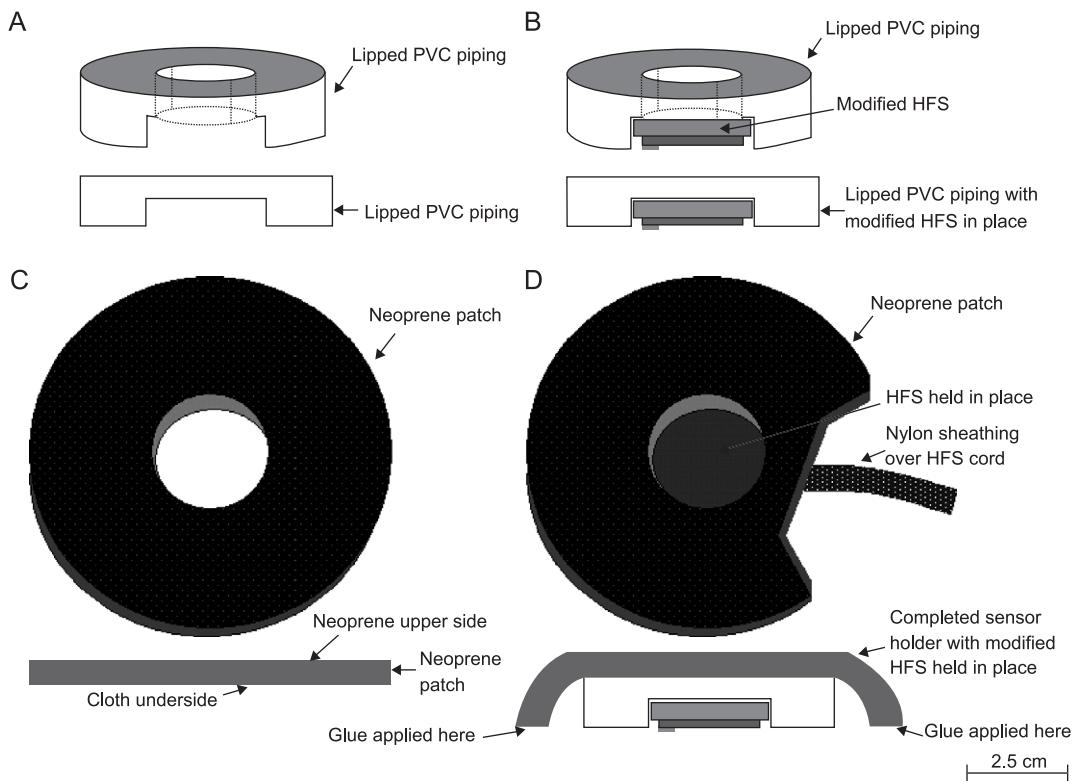


Fig. 2. Lipped PVC sensor holder piece (A), with modified HFS in place (B), neoprene patch (C), and completed sensor holder with modified HFS in place (D). All diagrams show three-dimensional or top (above) and corresponding side views (below).

diameter \times 0.5-cm thickness. A 3.0-cm diameter hole was cut from the center, and 3.0-cm openings were cut along the edge to facilitate placement and removal (Fig. 2D). The HFS was held firmly in place on bare skin due to the downward force of the lipped PVC and by gluing the neoprene patch to the fur surrounding the shaved area. No glue was applied to either the HFS or the bare skin surface of the animal.

2.1.2. Heat flux recorder

Heat flux data were recorded using a custom-built animal-borne heat flux recorder (HFR), built by M. Horning, measuring 13 \times 5 \times 2 cm. The device had 1 Mb memory, sampled up to eight sensor inputs sequentially at a 1-s rate and could sample for up to 6 consecutive days. The HFR could record output from up to four HFSs and four corresponding thermistors, resulting in a sampling rate of each sensor once every 8 s. HFS output was processed by an instrumentation grade preamplifier and output

from thermistors by an operational transimpedance amplifier. The amplified output voltage was digitized through a multiplexed 12-bit A/D converter. Data were stored on the HFR in digital format, corresponding to a range of zero to 4095 possible steps, with each step corresponding to a value of input in millivolts (mv). Programming and downloading of the HFR was accomplished via a custom optical interface to a laptop PC (Ancel et al., 1997; Horning and Trillmich, 1997) after each recording session. The HFR was attached to animals by means of an epoxy baseplate with a quick release attachment mechanism.

2.2. Calibration

Thermistors were calibrated by submerging HFSs in a temperature-controlled circulating water bath (VWR Scientific Products, model 1127) in 2 °C increments from 40 to 0 °C. Water temperatures

recorded with reference thermometers were used to derive calibration equations to convert recorder output directly to temperature in °C. HFSs were calibrated by the manufacturer according to methods outlined by the American Society of Testing Materials (ASTM), reviewed annually by the National Institute of Standards and Technology (NIST). Using this supplied calibration value, recorded A/D counts were first converted to millivolt values based on the input amplification factor and then converted to heat flux values using the supplied calibration factor and converted to SI units of W m⁻².

2.3. Animals

Two adult female Steller sea lions (*Eumetopias jubatus*) aged 9 years old, identified as FKI and FSU, were used for initial testing of the sensor holder design. Both animals had been captured as pups off British Columbia, Canada, and were housed in outdoor pools at the Alaska SeaLife Center (ASLC) in Seward, AK, USA. Animals were fed a daily diet of walleye pollock (*Theragra chalcogramma*) and herring (*Clupea harengus*) supplemented with vitamins. Morphometrics of the sea lions were measured throughout the course of data collection (May–August 2002). These included body mass, blubber thicknesses, straight total body length, and axillary, middle, and hip girths (Table 1). Blubber thicknesses were measured at four locations corresponding to subsequent HFS placement using a Sonosite portable ultrasound system, Sonosite 180 VET plus C60 abdominal transducer unit (Sonosite, Bothell, WA, USA) following the methods detailed in Mellish et al.

(2004). All experiments were conducted under Texas A&M University Laboratory Animal Care Committee AUP # 2001-112 and the ASLC's Institutional Animal Care and Use Committee AUP # 01-001 and MMPA permit # 881-1443.

Two adult female Weddell seals (*Leptonychotes weddellii*) identified as FTH and FLO were used to test the sensor holder design on wild, free-ranging animals. Both animals were captured off Ross Island, McMurdo Sound, Antarctica, in November 2002. All experimental procedures followed NIH guidelines and were conducted under Institutional Animal Care and Use Committee permits, MMPA permit # 821-1588 and Antarctic Conservation Act permit # 2002-003. Morphological measurements were collected from both animals. These included body mass, straight and curvilinear lengths, axillary girth, and blubber thicknesses (Table 1).

2.4. Attachment and experimental procedures

2.4.1. Steller sea lions

Sea lions were kept dry for at least 12 h prior to attachment procedures. Animals were placed under isoflurane (AErrane®, Baxter Healthcare, Deerfield, IL, USA) anesthesia for the duration of the attachment procedure, which lasted approximately 30 min. The fur was cleaned and dried with 70% isopropyl alcohol and acetone. A 3.0-cm diameter circle of fur was shaved at each of four locations chosen for HFS placement (Fig. 3). An epoxy baseplate with a quick release attachment mechanism for the HFR (13×5×2 cm) was glued to the fur on the dorsal midline of each animal just below the shoulder blades using

Table 1
Morphological data

Animal	Sex	n	Mass (kg)	Length (cm)		Girth (cm)			Blubber thickness (cm)			
				Straight	Curvilinear	Hips	Middle	Axillary	Hips	Middle	Axillary	Shoulder
<i>E. jubatus</i>												
FKI	F	3	191.8±4.7	220.0±2.3	n/m	92.7±1.2	128.5±4.3	141.0±1.7	1.47	1.76	1.73	1.29
FSU	F	2	195.5	222.0	n/m	92.0	129.0	140.0	1.74	1.97	1.93	1.80
<i>L. weddelli</i>												
FTH	F	1	366.6	224.0	242.5	n/m	n/m	192.5	4.35	n/m	6.80	4.91
FLO	F	1	435.6	253.0	274.0	n/m	n/m	196.0	3.38	n/m	6.43	4.74

F—female, n/m—not measured. Values are means±S.D.

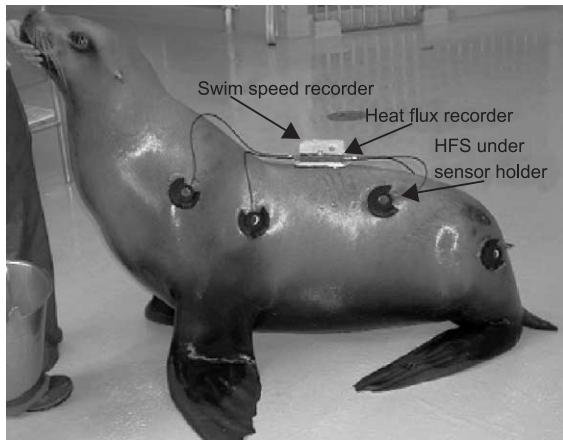


Fig. 3. Heat flux sensors, heat flux recorder, and swim speed recorder in place on study animal.

Everset® brand 10-set epoxy. The neoprene of the four sensor holders was glued to the fur surrounding the shaved patch of skin using Loctite QuickTite® cyanoacrylate gel. To account for potential differences in heat flux across the body of animals, an a priori decision was made to place two HFSs on areas of high heat flux and two HFSs on areas of low heat flux. These were called ‘hot spots’ and ‘cold spots,’ respectively, and were determined from thermal images taken for a concurrent study (Willis et al., 2004), using a FLIR Systems ThermaCAM® PM 695 thermal imaging camera (FLIR Systems, Boston, MA, USA). Once the baseplate and all sensor holders had set, the animal was removed from anesthesia and allowed to recover for 24 h before experiments began.

Experimental foraging sessions were conducted after placing the HFR and four HFSs into their baseplate and sensor holders, respectively, while the animal remained still under behavioral control. Once all sensors were in place (Fig. 3), animals were released into a large outdoor pool (600,000 l; 5.0-m depth; surface area 145 m²). Animals swam in waters of ambient temperature (mean=8.1±0.3 °C; range=7.5–8.6 °C) for between 4 and 9 min with the HFR and HFSs attached. Animals had been trained to conduct simulated foraging dives for a separate study, the methods of which are detailed in Cornick and Horning (2003). In brief, animals were trained to receive fish from three 4-in diameter plastic tubes

extending into the tank. Remote controlled behavioral conditioning lights near the fish releasing trap doors were used to elicit simulated foraging dives by the animals. Between 4.0 and 6.0 kg of fish were consumed throughout each foraging session. Eighteen separate foraging sessions were conducted, five of which consisted of the animal wearing a drag harness for a separate study that utilized drag-based modifications to assess locomotor cost (L. Cornick, unpublished data). Thus, of the 72 HFSs deployed, 20 were deployed in sessions where animals wore a harness. Upon completion of experimental sessions, the animals exited the water, and the HFR and HFSs were removed so that only the four sensor holders and the baseplate remained glued to their fur. All heat flux data were then downloaded from the HFR and analyzed using UMVIEW data analysis software (Mohren and Horning, 1996) and SPSS 10.0 for Windows (SPSS, 1999).

2.4.2. Weddell seals

Capture and sedation of animals, as well as attachment of recording devices, followed the procedure detailed in Williams et al. (2004). The attachment procedure of HFSs and sensor holders for Weddell seals was identical to that for Steller sea lions with a few exceptions. Unlike HFS attachment to Steller sea lions, HFSs were intended to remain on Weddell seals for the duration of HFR memory or approximately 6 days. As a result, a 3.0-cm opening in the neoprene holder ring for sensor removal was not required. Unlike the above-referenced study (Williams et al., 2004), seals were released as free-ranging animals near the capture site. After 6 days, animals were located using VHF telemetry and physically restrained without use of anesthesia while all HFSs, sensor holders, and the HFR were removed. All heat flux data were then downloaded from the HFR and analyzed using UMVIEW data analysis software (Mohren and Horning, 1996) and SPSS 10.0 for Windows (SPSS, 1999).

2.5. Exclusion criteria

To identify potentially problematic data sets resulting from mechanical stress damage to sensors, cables, and connectors or from sensors slipping from holders, a priori exclusion criteria were established

before the onset of primary data analysis. These criteria were defined by physiologically improbable, extreme conditions. Skin temperature data were excluded above 40 °C or below a temperature value equal to half of known water temperature. Temperature data were also excluded if ΔT exceeded ± 5.0 °C within a single sampling period of 8 s, except when the animal entered or exited the water. Heat flux data were excluded if heat flux instantaneously changed by more than 150% of the initial change observed when the animal first entered the water. For both heat flux and skin temperature, data were excluded if it appeared that sensors were no longer properly placed, as indicated by skin temperature values dropping instantaneously to water temperature and heat flux values simultaneously decreasing to

near zero. All trials were visually scanned using UMVIEW imaging software (Mohren and Horning, 1996) (Fig. 4) and checked according to these criteria.

2.6. Effects of HFSs and attachment mechanism

To test for effects of HFSs and the attachment mechanism on heat flux, a test rig was constructed to allow for experiments under controlled conditions. A 46×28×60 cm rectangular box was placed into a temperature and current-controlled swim flume located at the Vancouver Aquarium Marine Science Centre (Vancouver, British Columbia, Canada) and stabilized so that its bottom third was submerged (Fig. 5). A detailed description of the swim flume is

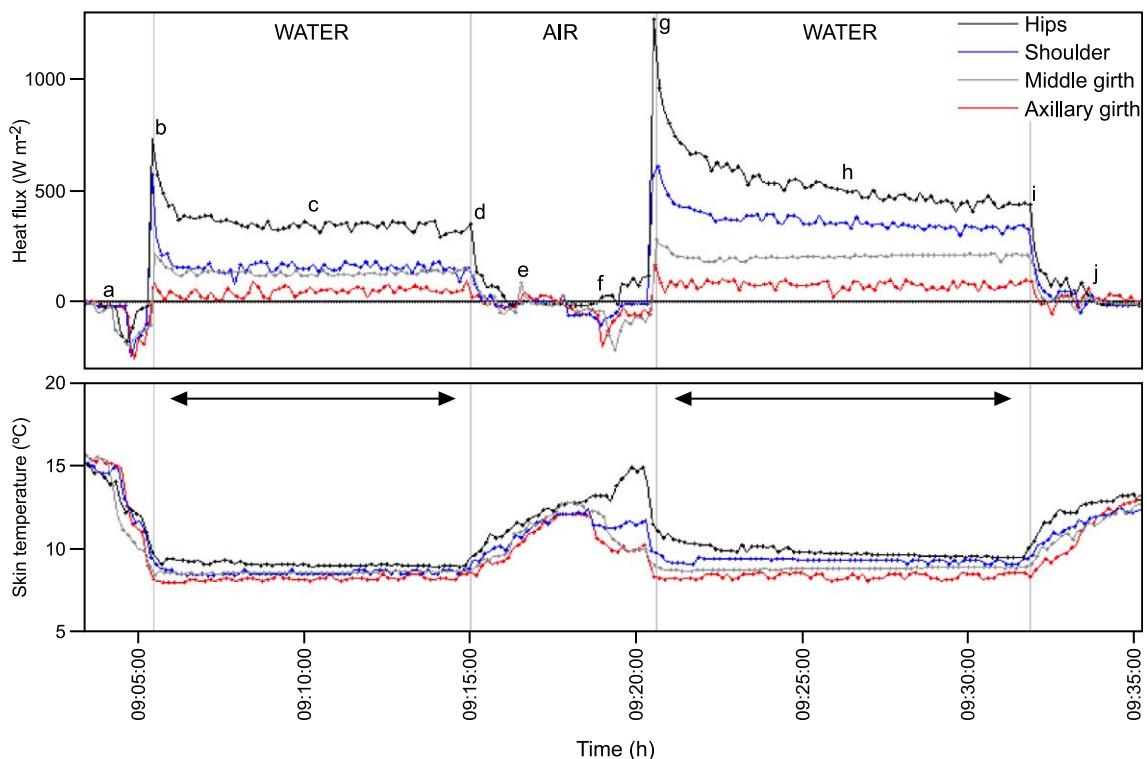


Fig. 4. Representative data record of swimming animals FKI and FSU. The four colored lines represent the different locations of HFS placement. The data streams begin recording with the HFSs in air and continue as they are placed on animal FSU (a), it enters the water (b), swims throughout the habitat (c), exits the water (d), HFSs are removed (e), HFSs are placed on animal FKI (f), it enters the water (g), swims throughout the habitat (h), exits the water (i), and HFSs are removed (j). Upon entering the water, heat flux at all locations increases with differences between locations, while skin temperature values simultaneously drop. The two areas between the vertical lines represent the segments of the record analyzed.

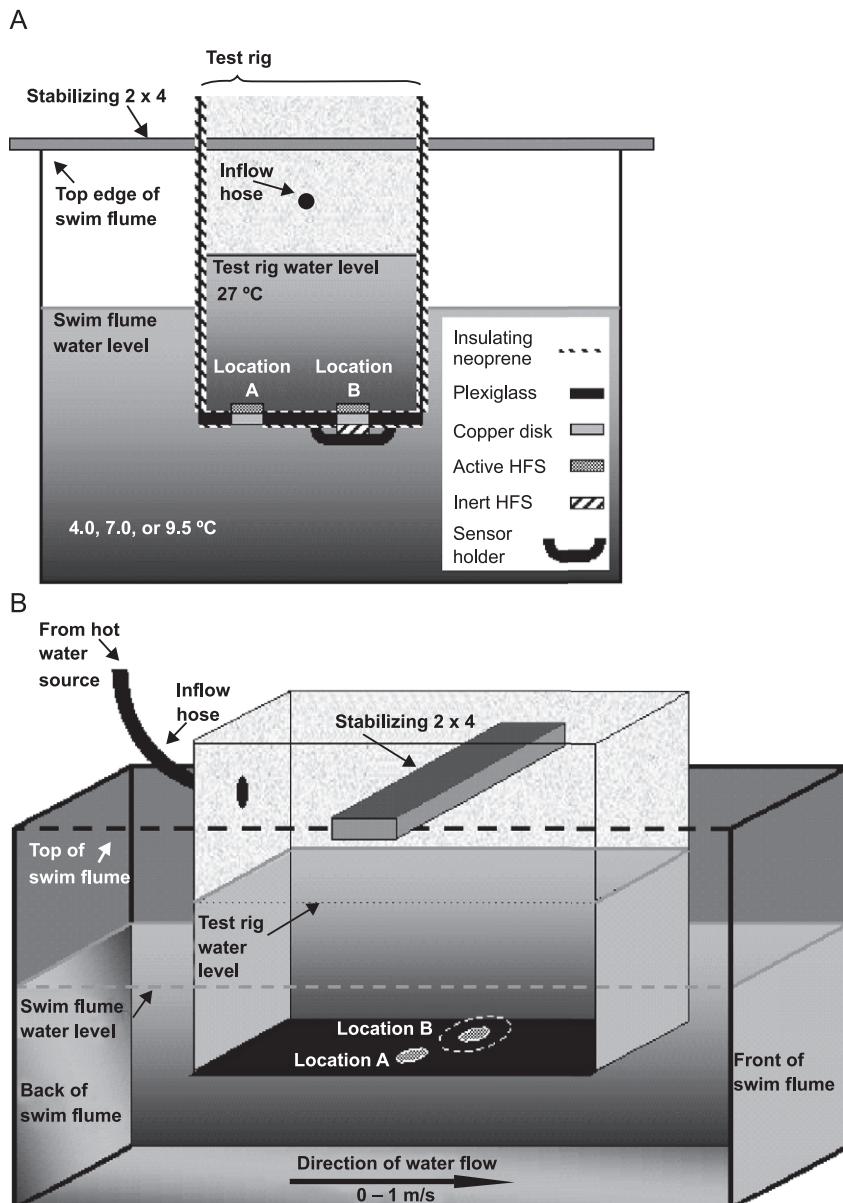


Fig. 5. Schematic of the test rig used to test for effects of the HFS and attachment mechanism from front (A) and three-dimensional (B) views. The bottom third of the test rig is submerged within a large temperature and current-controlled swim flume. HFSs placed inside on the bottom of the test rig measure heat flux across a bare copper disk serving as a control (location A) and a copper disk with the designed attachment mechanism and HFS in place (location B). Water temperature in the test rig is kept constant at 27 °C, and measurements of heat flux are made at three water temperatures and five water flow speeds. Drawings of test rig and swim flume not to scale.

available in Rosen and Trites (2002). The sides of the box were constructed from plywood that had been finished and sealed. The bottom of the box consisted of a Plexiglas sheet into which two copper

disks ($k=400 \text{ W m}^{-1} \text{ °C}^{-1}$) of 25-mm diameter and 5-mm thickness were inserted at locations A and B. Two functional HFSs were attached to the copper disks on the inside of the box with a thin layer of

thermally conductive paste (CircuitWorks CT40-5 by Chemtronix, Kennesaw, GA, USA), and these were used to measure heat flux at locations A and B. On the underside (swim flume side) of the box, location A was bare and served as a control. At location B, a disconnected HFS was held in place over the copper disk by the designed sensor holder. The remaining area of the Plexiglas sheet and all sides of the box were insulated on both sides with 3-ml open cell neoprene. An inflow hose from a hot water source was connected to the upstream side of the test rig. Heat flux between the internal compartment and swim flume was measured in 10-min increments at water temperatures of 4.0, 7.0, and 9.5 °C and flow speeds of 0, 0.2, 0.4, 0.8, and 1.0 m/s. The water temperatures were chosen to reflect the range of temperatures that most Steller sea lions inhabit (Stabeno et al., 2001; Benson and Trites, 2002). Water temperature inside the test rig was set to a constant inflow temperature of 27 °C rather than the body core temperature in live sea lions of 37 °C to achieve comparable amounts of heat flux across the highly conductive copper disks to values recorded during initial animal trials.

A mathematical relationship between heat flux uninfluenced by the HFS and heat flux with the HFS and attachment mechanism was established by linear regression analysis and analysis of covariance (ANCOVA). ANCOVAs were performed separately for heat flux data collected at 7.0 and 9.5 °C to test for the effects of different treatments and water flow speeds. Coefficients from linear regressions were used to establish linear equations, and when significant, differences in intercepts were compared to calculate both a percent difference between treatments and an appropriate correction factor for data collected using the designed attachment mechanism. Data from tests at 4.0 °C were excluded from ANCOVA because the particular HFS used at location A had extremely sensitive calibrations. As a result of this sensitivity, the HFR permissible input range of sensor voltages for the preamplifier was exceeded at heat flux values obtained for speeds above 0.2 m/s, and further increases in heat flux resulted in no changes in A/D values. However, at 4.0 °C, data were available for locations A and B at speeds of 0–0.2 m/s and were qualitatively compared to results from ANCOVAs at 7.0 and 9.5 °C.

3. Results

3.1. Attachment design

3.1.1. Steller sea lions

Seven and 11 separate foraging sessions were conducted with animals FKI and FSU, respectively, resulting in a total of 18 sessions. Four HFSs were placed in their respective sensor holders throughout all foraging sessions, resulting in a total of 72 deployed HFSs. For animal FKI, mean session duration was 6.8 min, and a total of 28 HFSs were deployed. Of these, none broke or fell out of their holders, and heat flux and skin temperature data were collected from all HFSs, resulting in an individual success rate of 100% for animal FKI. For animal FSU, mean session duration was 5.8 min, and a total of 44 HFSs were deployed, 20 of which were during sessions with added sources of hydrodynamic drag. Of these, none broke, and two fell out of their sensor holders, resulting in an individual success rate of 95%. For both animals combined, HFSs fell out of their holders twice, resulting in the successful retrieval of heat flux and skin temperature data from a total of 70 HFSs or 97% of all HFSs deployed on Steller sea lions. All sensor holders remained on both animals for 7 weeks following the attachment procedure. During the 8th week, sensor holders began to lift from the fur, and data collection was terminated. For animal FKI, heat flux corrected for effects of the thermal resistance of HFSs and attachment mechanism ranged from 138.6 to 2065.6 W m⁻² ($n=28$) across all locations where HFSs were placed, with a mean \pm S.E.M. of 952.2 ± 99.3 W m⁻² ($n=28$). For animal FSU, corrected heat flux ranged from 178.4 to 1735.7 W m⁻² ($n=22$) across all locations, with a mean \pm S.E.M. of 779.9 ± 93.1 W m⁻² ($n=22$). Reported heat flux values for animal FSU do not include results from foraging sessions with added sources of hydrodynamic drag.

3.1.2. Weddell seals

Four HFSs were placed in their holders for both animal deployments, resulting in a total of eight deployed HFSs on free-ranging seals. For animal FTH, deployment duration was 7 days, and no HFSs broke or fell out, resulting in an individual success rate of 100%. For animal FLO, deployment duration was also 7 days, and no HFSs fell out, but one was

severed at the cord-sensor interface at the end of the 5th day of deployment, leaving the actual HFS still in place under the sensor holder but without connection to the HFR. Prior to severing, heat flux data were successfully collected from this sensor for 5 of the 6 days of HFR memory availability. This was therefore included as a successful but truncated deployment, resulting in an individual success rate of 100% for animal FLO. Overall, heat flux and skin temperature data were collected from a total of eight HFSs or 100% of all HFSs deployed on Weddell seals. All sensor holders remained on both animals for the 1-week duration of their deployment, at which point they were manually removed upon animal recapture. Heat flux data were analyzed from two dives for animal FTH and one dive for animal FLO. For animal FTH, corrected heat flux values ranged from 574.6 to 1442.5 W m⁻² ($n=8$) across all locations, with a mean \pm S.E.M. of 1021.9 ± 109.3 W m⁻² ($n=8$). For animal FLO, corrected heat flux ranged from 875.2 to 1866.2 W m⁻² ($n=4$) across all locations, with a mean \pm S.E.M. of 1395.9 ± 262.0 W m⁻² ($n=4$).

3.2. Effects of HFSs and attachment mechanism

Differences in heat flux between treatments were consistent, and heat flux decreased with increasing water temperatures at all flow speeds (Fig. 6). Heat flux from location A was always greater than heat flux from location B and differed slightly in magnitude

depending on water temperature and flow speed. Heat flux at a water temperature of 7.0 °C increased approximately linearly with water flow speed at location A (least squares linear regression, $F_{1,3}=169.5$, $p=0.001$, $r^2=0.98$; Fig. 6) and location B (least squares linear regression, $F_{1,3}=96.7$, $p=0.002$, $r^2=0.97$; Fig. 6). There were no differences between slopes of regression lines at locations A and B (ANCOVA, $F_{1,7}=3.9$, $p=0.10$), but intercepts were significantly different (ANCOVA, $F_{1,7}=2814.9$, $p<0.001$), with heat flux from location B being a reduction of approximately 75% from location A regardless of flow speed.

Heat flux at a water temperature of 9.5 °C increased with water flow speed at location A (least squares linear regression, $F_{1,3}=0.63$, $p=0.49$, $r^2=0.17$; Fig. 6) but exhibited no change at location B (least squares linear regression, $F_{1,3}=3.5$, $p=0.16$, $r^2=0.53$; Fig. 6) and did not change significantly with water flow speed at either location. There were no differences between slopes of regression lines at locations A and B (ANCOVA, $F_{1,7}=0.166$, $p=0.70$), but intercepts were significantly different (ANCOVA, $F_{1,7}=52.1$, $p<0.001$), with heat flux from location B a reduction of approximately 69% from location A regardless of flow speed. At 4.0 °C and water flow speeds of 0 and 0.2 m/s, heat flux from location B was a reduction of 67% and 62% from location A, respectively, and exhibited a mean reduction of 65% for both speeds combined. Overall, the effects of the

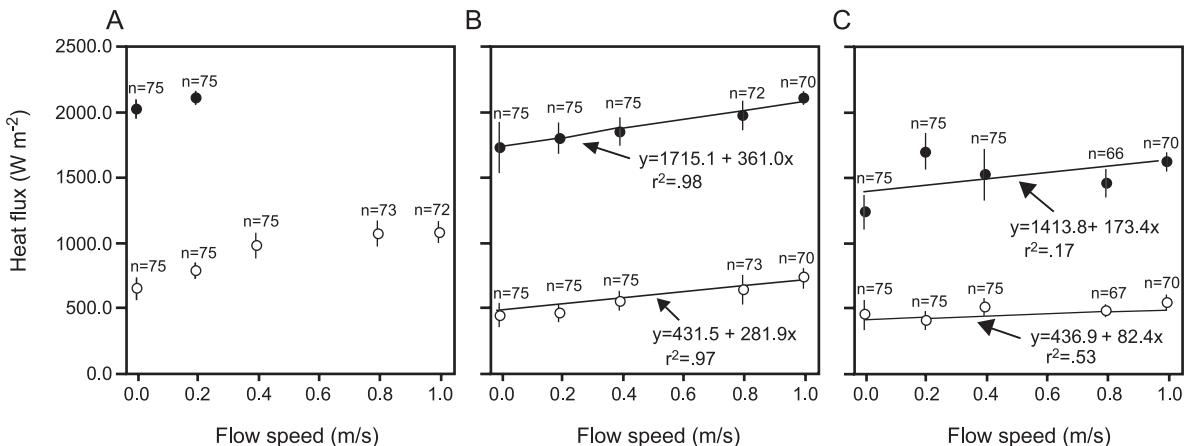


Fig. 6. Results of heat flux measurements from the test rig in waters of 4.0 °C (A), 7.0 °C (B), and 9.5 °C (C) at location A (control, ●) and location B (HFS+attachment mechanism, ○). Each point represents mean heat flux measured over a 10-min period \pm S.D. at each flow speed. Least squares linear regressions are indicated by solid lines through the data points and accompanying equations.

attachment mechanism were insulative and reasonably consistent across water temperatures and flow speeds with, on average, heat flux from location B being a reduction of approximately 70% from location A. Heat flux measured at location B was, on average, approximately 30% of the actual heat flux at location A, resulting in a correction factor of 3.42. This correction factor was applied to all measurements of heat flux from animal experiments to account for the thermal resistance of HFSs and insulative effects of the attachment mechanism.

4. Discussion

Previous studies on stationary marine mammals have used HFSs to measure heat flux (e.g., Ohata and Whittow, 1974; McGinnis, 1975; Kvadsheim and Folkow, 1997; Noren et al., 1999; Williams et al., 1999; Meagher et al., 2002), but this study's application is the first such use on swimming and free-ranging pinnipeds. Sensor holders glued onto dry fur of Weddell seals and Steller sea lions allowed for data collection ranging from 7 days to several weeks, with minimal handling of animals for attachment and removal. The sensor holder design allowed HFSs to be held firmly to the skin without the use of glues to either the skin of the animal or the HFS itself. Results also indicated that the sensors withstood effects of extreme temperatures and increased pressure resulting either from depth during dives or the large masses of Weddell seals (366.6–435.6 kg) when hauled out. A limitation to the success of the attachment design was that it appeared to be dependent on the behavior and flexibility of individual study animals. Whereas both female Steller sea lions at the ASLC took no notice of the HFSs and sensor holders while swimming or hauled out, an adult male used in an earlier pilot study bit and chewed them off. These included sensor holders at the hips, middle girth, and, in some cases, axillary girth regions, as these were the areas most flexibly accessible. Neither of the seals in Antarctica appeared to notice either the HFSs or HFR, and upon removal, the HFSs and HFR showed no signs of having been bitten or chewed.

Results from the test rig indicated that there are considerable effects of the HFS and sensor holder attachment mechanism on heat flux output, and that a

correction factor must be incorporated (Fig. 6). Our experiments showed that the thermal resistance provided by HFSs along with insulation from the attachment mechanism caused underestimations of heat flux rates by approximately 70%. Thus, measurements of heat flux collected using HFSs in conjunction with our designed attachment mechanism must be corrected by a factor of 3.42. Although this correction factor is significantly higher than anticipated, Wissler and Ketch (1982) estimated that differences of 15–20% between actual and measured heat flux could occur in water due to the thermal resistance of HFSs. In addition, in calibration experiments conducted by Kvadsheim and Folkow (1997), the thermal resistance of the HFSs caused underestimations in heat flux of between 4% and 11% at heat flux rates between 50 and 150 W m^{-2} , respectively, and they suggested a correction factor of approximately 1.18. In the present study, results from pilot experiments on effects of HFSs conducted without water flow and excluding the attachment mechanism were similar to those of Kvadsheim and Folkow (1997) and suggested a correction factor of 1.23 (Willis, 2004). However, these studies accounted only for the HFSs themselves, not additional attachment mechanisms as in the present study. We estimate that the thermal resistance of the HFSs themselves account for approximately 28–31% of the discrepancy, with insulative effects of the sensor holder accounting for the other 69–72%. Although the insulative effects of HFSs and our attachment mechanism are large, they are also consistent, allowing for the incorporation of a relatively simple correction factor to take these effects into account.

Heat flux measurements made using HFSs vary widely both within and between pinniped species (Table 2), and corrected values from the present study are among the highest reported in the literature. Of the studies listed in Table 2, only Kvadsheim and Folkow (1997) report correcting for the thermal resistance of HFSs. Reported values of heat flux also differ depending on the medium and temperature in which measurements were made, age and body mass, and the location of HFS placement. Comparisons across species are therefore difficult given the range of measurement conditions, further supporting the utility of a reliable and easily replicated measurement technique. To assess the validity of the comparably high heat flux values reported here, measurements were compared to meas-

Table 2

Direct measurements of heat flux in pinnipeds obtained using HFSs

Family/species	n	Age	Temperature (°C)		Heat flux (W m ⁻²)			Reference
			Air	Water	Location	Mean	Range	
<i>Otariidae</i>								
Steller sea lion (<i>Eumetopias jubatus</i>)	14	Adult		7.5–8.6	C	518.2	138.6–879.4	Present study [†]
	11	Adult		7.5–8.6	C	509.4	178.4–970.4	Present study [†]
	14	Adult		7.5–8.6	H	1386.2	1041.1–2065.6	Present study [†]
	11	Adult		7.5–8.6	H	1050.4	518.2–1735.7	Present study [†]
	28	Adult		7.5–8.6	A	952.2	138.6–2065.6	Present study [†]
	22	Adult		7.5–8.6	A	779.9	178.4–1735.7	Present study [†]
Northern fur seal (<i>Callorhinus ursinus</i>)	53	Adult	U		U		74.1–350.0	T. Williams, unpublished data
	3	Pup	6		B		500.0–600.0	Blix et al., 1979
California sea lion (<i>Zalophus californianus</i>)	14	U	30		U	56.0	37.0–79.0	Ohata and Whittow, 1974
<i>Phocidae</i>								
Weddell seal (<i>Leptonychotes weddellii</i>)	4	Adult		2.0–3.0	C	809.7	574.6–1148.5	Present study [†]
	2	Adult		2.0–3.0	C	944.9	574.6–1148.5	Present study [†]
	4	Adult		2.0–3.0	H	1234.1	949.0–1442.5	Present study [†]
	2	Adult		2.0–3.0	H	1846.9	1827.5–1866.2	Present study [†]
	8	Adult		2.0–3.0	A	1020.9	574.6–1442.5	Present study [†]
	4	Adult		2.0–3.0	A	1395.9	875.2–1866.2	Present study [†]
Northern elephant seal (<i>Mirounga angustirostris</i>)	11	Pup	11.0–19.0		B	163.5	14.4–359.6	McGinnis, 1975
	11	Pup	11.0–19.0		F	318.4	14.4–647.3	McGinnis, 1975
	1	Adult	17.0		B	169.8		McGinnis, 1975
	1	Adult	17.0		F	148.9		McGinnis, 1975
Harbor seal (<i>Phoca vitulina</i>)	14	U	30.0		U	33.0	12.0–87.0	Ohata and Whittow, 1974
Harp seal (<i>Phoca groenlandica</i>)	3	Pup		1.0–2.0	B		90.0–110.0	Kvadsheim and Folkow, 1997
	3	Pup		1.0–2.0	F		10.0–30.0	Kvadsheim and Folkow, 1997
	3	Pup		14.0–15.0	B		45.0–90.0	Kvadsheim and Folkow, 1997
	3	Pup		14.0–15.0	F		15.0–25.0	Kvadsheim and Folkow, 1997
	3	Pup		23.0–24.0	B		30.0–130.0	Kvadsheim and Folkow, 1997
	3	Pup		23.0–24.0	F		60.0–370.0	Kvadsheim and Folkow, 1997

C—cold spots; H—hot spots; A—all locations combined; B—body trunk, general; F—flipper; U—unknown.

[†] Swimming animals.

ured metabolic rates for Steller sea lions (Rosen and Trites, 2003) and Weddell seals (Kooyman et al., 1973; Castellini et al., 1992) from past studies. Since no published studies have directly measured heat flux in swimming pinnipeds, measurements from the present study were converted to units of metabolic rate in W by

estimating surface area of sea lions (Roscow, 2001) and seals (Innes et al., 1990). In all referenced studies, measurements of metabolic rate were collected from immobile, resting animals, and model predictions also assumed animals were stationary. Thus, neither measurements nor estimates included additional heat pro-

duction due to locomotor activity. To account for additional heat generated by locomotion, locomotor cost (LC), defined as the minimum cost of transport minus maintenance costs (Williams, 1999a; Rosen and Trites, 2002), was calculated based on experimentally determined allometric equations for Steller sea lions (Rosen and Trites, 2002) and Weddell seals (Williams et al., 2004) and incorporated into estimates of metabolic rate. Heat flux averages from hot and cold spots from the present study resulted in metabolic rate estimates approximately 1.9 and 3.7 times higher than published metabolic rates including additional heat generated by locomotion for Steller sea lions and Weddell seals, respectively (see Appendix A for calculations).

However, values of heat flux used for comparison in the present study were arithmetic means of measurements collected from all locations along the body trunk, and it is unlikely that hot and cold spots are evenly distributed on both spatial and temporal scales among or between individual animals. Indeed, detailed analyses of thermal images of hauled out seals have shown that thermal windows are neither constant in space nor time (Mauck et al., 2003). In addition, results from thermal image analysis on Steller sea lions indicate that hot spots comprise less than half of the surface area of the animal (Willis, 2004). These studies suggest that thermal windows do not contribute equally to overall heat loss from either phocids or otariids, and that means used to estimate metabolic rate in the present study were likely inflated due to heat flux values from hot spots having been considered equally. When mean heat flux values from cold spots only were converted to units of metabolic rate, results from the present study were almost identical to measured metabolic rates including heat generated by locomotion for Steller sea lions and approximately 2.6 times higher for Weddell seals. The reason for the difference in Weddell seals is not known; however, locations chosen as representative cold spots were based on locations chosen for Steller sea lions. Since thermal windows in phocids have been shown to change both temporally and spatially (Mauck et al., 2003), our ‘cold spot’ placements may not have been the coldest areas on the animals at any given time. Indeed, thermal images taken of hauled out Weddell seals do not appear to show consistent thermal windows along the body trunk (T. Williams,

personal communication) like those observed in Steller sea lions (Willis et al., 2004). However, this remains to be tested and is likely complicated by the relationship between exercise and cold water, including the network of interactions between insulation, body mass, peripheral blood flow, exercise level, behavior (i.e., swimming versus diving), and water temperature (MacArthur, 1989; Noren et al., 1999; Williams et al., 1999).

5. Conclusions

The design for HFS attachment developed for this study enabled the collection of heat flux data from swimming and stationary phocids and otariids in air and water with one and the same methodology. The design also allowed for the continuous collection of heat flux data from captive and free-ranging pinnipeds for periods ranging from 4 min to 7 days. Such data were previously unobtainable for pinnipeds without direct human manipulation during experiments, as no design existed that allowed for independent and long-term or removable HFS attachment. Results from the present study suggest that HFSs can be deployed with success and minimal handling on free-ranging pinnipeds, allowing for the direct measurement of heat flux in wild, foraging animals. Finally, the importance of ground-truthing measurements made by external devices cannot be underestimated, and we suggest that future studies that utilize this or similar designs incorporate a correction factor based on water temperature and flow speeds where appropriate.

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Appendix A

Table A1

List of symbols and values

Symbol	Parameter	Unit
BM	Body mass	kg
DD	Dive duration	min
HF	Heat flux	W m^{-2}
LC	Locomotor cost	J m^{-1}
MR	Metabolic rate	W
RMR	Resting metabolic rate	W
SA	Surface area	m^2
S_n	Stroke number	
SS	Swim speed	m s^{-1}

A.1. Heat flux to metabolic rate calculations

A.1.1. Steller sea lions (present study)

All locations:

$$\begin{aligned}\text{MR}_{\text{FKI}} &= (952.2 \text{ W m}^{-2} \times 1.587 \text{ m}^2) = 1511.1 \text{ W} \\ \text{MR}_{\text{FSU}} &= (779.9 \text{ W m}^{-2} \times 1.863 \text{ m}^2) = 1453.0 \text{ W} \\ \text{Mean} &= 1482.1 \text{ W}\end{aligned}$$

Cold spots only:

$$\begin{aligned}\text{MR}_{\text{FKI}} &= (518.2 \text{ W m}^{-2} \times 1.587 \text{ m}^2) = 822.4 \text{ W} \\ \text{MR}_{\text{FSU}} &= (509.4 \text{ W m}^{-2} \times 1.863 \text{ m}^2) = 949.0 \text{ W} \\ \text{Mean} &= 885.7 \text{ W}\end{aligned}$$

A.1.2. Weddell seals (present study)

All locations:

$$\begin{aligned}\text{MR}_{\text{FTH}} &= (1021.9 \text{ W m}^{-2} \times 2.370 \text{ m}^2) = 2422.0 \text{ W} \\ \text{MR}_{\text{FLO}} &= (1395.9 \text{ W m}^{-2} \times 2.590 \text{ m}^2) = 3618.9 \text{ W} \\ \text{Mean} &= 3020.5 \text{ W}\end{aligned}$$

Cold spots only:

$$\begin{aligned}\text{MR}_{\text{FTH}} &= (809.7 \text{ W m}^{-2} \times 2.370 \text{ m}^2) = 1919.0 \text{ W} \\ \text{MR}_{\text{FLO}} &= (944.9 \text{ W m}^{-2} \times 2.590 \text{ m}^2) = 2447.3 \text{ W} \\ \text{Mean} &= 2183.2 \text{ W}\end{aligned}$$

A.2. Measured metabolic rates from other studies

A.2.1. Steller sea lions

Source: [Rosen and Trites, 2003](#)

$\text{RMR}=64,500 \text{ ml O}_2 \text{ h}^{-1}=359.8 \text{ W}$, where RMR is mean value from postprandial animals in 8 °C water; body mass is 159 kg; age is 3 years.

A.2.2. Weddell seals

Source: [Castellini et al., 1992](#)

$\text{RMR}=4.1 \text{ ml O}_2 \text{ min}^{-1}=486.4 \text{ W}$, where RMR is mean value, likely from postprandial animals; mean body mass is 355 kg; age, adult.

Source: [Kooyman et al., 1973](#)

$\text{RMR}=5.1 \text{ ml O}_2 \text{ min}^{-1}=725.5 \text{ W}$, where RMR is mean value, likely from postprandial animals; mean body mass is 425 kg; age, adult.

Mean measured RMR=607.0 W

A.3. Calculations of locomotor cost

A.3.1. Steller sea lions

Source: [Rosen and Trites, 2002](#)

$\text{LC}=1.651 \times \text{BM}^{1.01}=337 \text{ J m}^{-1}$; for an animal swimming 1.3 m/s (see [Willis et al., 2004](#)), this is equivalent to 438.1 W, where BM=193.7 kg or mean mass of animals FKI and FSU.

A.3.2. Weddell seals

Source: [Williams et al., 2004](#)

$\text{LC}=(-3.78+0.04 S_n)=37.4 \text{ ml O}_2 \text{ kg}^{-1}=221.2 \text{ W}$, where $S_n=51.6 \text{ DD}-139.2=1029.5$; DD=22.7 min, or mean dive duration of FTH and FLO; BM=401.1 kg, or mean mass of animals FTH and FLO.

References

- Ancel, A., Horning, M., Kooyman, G.L., 1997. Prey ingestion revealed by oesophagus and stomach temperature recordings in cormorants. *J. Exp. Biol.* 200, 149–154.
 Bartholomew, G.A., Wilke, F., 1956. Body temperature in the northern fur seal, *Callorhinus ursinus*. *J. Mammal.* 37, 327–337.

- Benson, A.J., Trites, A.W., 2002. Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. *Fish Fish.* 3, 95–113.
- Bligh, J., Johnson, K.G., 1973. Glossary of terms for thermal physiology. *J. Appl. Physiol.* 35, 941–961.
- Blix, A.S., Miller, L.K., Keyes, M.C., Grav, H.J., Elsner, R., 1979. Newborn northern fur seals (*Callorhinus ursinus*)—do they suffer from cold? *Am. J. Physiol.* 236, R322–R327.
- Boily, P., 1995. Theoretical heat flux in water and habitat selection of phocid seals and beluga whales during the annual molt. *J. Theor. Biol.* 172, 235–244.
- Boily, P., Lavigne, D.M., 1996. Thermoregulation of juvenile grey seals, *Halichoerus grypus*, in air. *Can. J. Zool.* 74, 201–208.
- Boily, P., Kvadsheim, P.H., Folkow, L.P., 2000. Cutaneous heat flux models do not reliably predict metabolic rates of marine mammals. *J. Theor. Biol.* 207, 317–323.
- Boyd, I.L., 2000. Skin temperatures during free-ranging swimming and diving in Antarctic fur seals. *J. Exp. Biol.* 203, 1907–1914.
- Campbell, G.S., 1977. An Introduction to Environmental Biophysics. Springer-Verlag, New York.
- Castellini, M.A., Kooyman, G.L., Ponganis, P.J., 1992. Metabolic rates of freely diving Weddell seals: correlations with oxygen stores, swim velocity and diving duration. *J. Exp. Biol.* 165, 181–194.
- Cornick, L.A., Horning, M., 2003. A test of hypotheses based on optimal foraging considerations for a diving mammal using a novel experimental approach. *Can. J. Zool.* 81, 1799–1807.
- Donohue, M.J., Costa, D.P., Goebel, M.E., Baker, J.D., 2000. The ontogeny of metabolic rate and thermoregulatory capabilities of northern fur seal, *Callorhinus ursinus*, pups in air and water. *J. Exp. Biol.* 203, 1003–1016.
- Ducharme, M.B., Frim, J., Tikuvisis, P., 1990. Errors in heat flux measurements due to the thermal resistance of heat flux disks. *J. Appl. Physiol.* 69, 776–784.
- Folkow, L.P., Blix, A.S., 1989. Thermoregulatory control of expired air temperature in diving harp seals. *Am. J. Physiol.* 257, R306–R310.
- Gallivan, G.J., Ronald, K., 1979. Temperature regulation in freely diving harp seals (*Phoca groenlandica*). *Can. J. Zool.* 57, 2256–2263.
- Gentry, R.L., 1973. Thermoregulatory behavior of eared seals. *Behaviour* 46, 73–93.
- Hansen, S., Lavigne, D.M., 1997. Ontogeny of the thermal limits in the harbor seal (*Phoca vitulina*). *Physiol. Zool.* 70, 85–92.
- Hansen, S., Lavigne, D.M., Innes, S., 1995. Energy metabolism and thermoregulation in juvenile harbor seals (*Phoca vitulina*) in air. *Physiol. Zool.* 68, 290–315.
- Hokkanen, J.E.I., 1990. Temperature regulation of marine mammals. *J. Theor. Biol.* 145, 465–485.
- Horning, M., Trillmich, F., 1997. Ontogeny of diving behavior in the Galapagos fur seal. *Behaviour* 134, 1211–1257.
- Innes, S., Worthy, G.A.J., Lavigne, D.M., Ronald, K., 1990. Surface areas of phocid seals. *Can. J. Zool.* 68, 2531–2538.
- Irving, L., Hart, J.S., 1957. The metabolism and insulation of seals as bare-skinned mammals in cold water. *Can. J. Zool.* 35, 497–511.
- Irving, L., Peyton, L.J., Bahn, C.H., Peterson, R.S., 1962. Regulation of temperature in fur seals. *Physiol. Zool.* 35, 275–284.
- Kooyman, G.L., Kerem, D.H., Campbell, W.B., Wright, J.J., 1973. Pulmonary gas exchange in freely diving Weddell seals. *Respir. Physiol.* 17, 283–290.
- Kvadsheim, P.H., Folkow, L.P., 1997. Blubber and flipper heat transfer in harp seals. *Acta Physiol. Scand.* 161, 385–395.
- Kvadsheim, P.H., Folkow, L.P., Blix, A.S., 1996. Thermal conductivity of minke whale blubber. *J. Therm. Biol.* 21, 123–128.
- Leyton, L., 1975. Fluid Behaviour in Biological Systems. Clarendon Press, Oxford.
- Liao, J.A., 1990. An investigation of the effect of water temperature on the metabolic rate of the California sea lion (*Zalophus californianus*). MS thesis. Department of Marine Sciences, University of California Santa Cruz, Santa Cruz, 55 pp.
- MacArthur, R.A., 1989. Aquatic mammals in cold. In: Wang, L.C.H. (Ed.), Advances in Comparative and Environmental Physiology. Springer-Verlag, Berlin, Heidelberg, pp. 289–325.
- Mauck, B., Bilgmann, K., Jones, D.D., Eysel, U., Dehnhardt, G., 2003. Thermal windows on the trunk of hauled-out seals: hot spots for thermoregulatory evaporation? *J. Exp. Biol.* 206, 1727–1738.
- McGinnis, S.M., 1975. Peripheral heat exchange in phocids. *Rapp. P.-V. Réun.* 169, 481–486.
- McGinnis, S.M., Ingram, D.L., 1974. Use of heat-flow meters to estimate rate of heat loss from animals. *J. Appl. Physiol.* 37, 443–446.
- Meagher, E.M., McLellan, W.A., Westgate, A.J., Wells, R.S., Frierson, D., Pabst, D.A., 2002. The relationship between heat flow and vasculature in the dorsal fin of wild bottlenose dolphins *Tursiops truncatus*. *J. Exp. Biol.* 205, 3475–3486.
- Mellish, J.E., Tuomi, P.A., Horning, M., 2004. Assessment of ultrasound imaging as a non-invasive measure of blubber thickness in pinnipeds. *J. Zoo Wildl. Med.* 35, 116–118.
- Mitchell, J.W., 1976. Heat transfer from spheres and other animal forms. *Biophys. J.* 19, 561–569.
- Mohren, W., Horning, M., 1996. UMview User's Guide. Ultramarine Instruments, Galveston.
- Noren, D.P., 2002. Thermoregulation of weaned northern elephant seal (*Mirounga angustirostris*) pups in air and water. *Physiol. Biochem. Zool.* 75, 513–523.
- Noren, D.P., Williams, T.M., Berry, P., Butler, E., 1999. Thermoregulation during swimming and diving in bottlenose dolphins, *Tursiops truncatus*. *J. Comp. Physiol., B* 169, 93–99.
- Ohata, C.A., Whittow, G.C., 1974. Conductive heat loss to sand in California sea lions and a harbor seal. *Comp. Biochem. Physiol.* 47A, 23–26.
- Pabst, D.A., Rommel, S.A., McLellan, W.A., 1999. The functional morphology of marine mammals. In: Reynolds III, J.E., Rommel, S.A. (Eds.), Biology of Marine Mammals. Smithsonian Institution Press, Washington, pp. 15–72.
- Roscow, E., 2001. Thermoregulation in Steller sea lions: a modelling approach. MS thesis. Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, 130 pp.

- Rosen, D.A.S., Trites, A.W., 2002. Cost of transport in Steller sea lions, *Eumetopias jubatus*. Mar. Mamm. Sci. 18, 513–524.
- Rosen, D.A., Trites, A.W., 2003. No evidence for bioenergetic interaction between digestion and thermoregulation in Steller sea lions (*Eumetopias jubatus*). Physiol. Biochem. Zool. 76, 899–906.
- Scholander, P.F., Schevill, W.E., 1955. Counter-current vascular heat exchange in the fins of whales. J. Appl. Physiol. 8, 279–282.
- SPSS, 1999. SPSS Advanced Models 10.0. SPSS, Chicago.
- Stabeno, P.J., Bond, N.A., Kachel, N.B., Salo, S.A., Schumacher, J.D., 2001. On the temporal variability of the physical environment over the south-eastern Bering Sea. Fish. Oceanogr. 10, 81–98.
- Tarasoff, F.J., Fisher, D.H., 1970. Anatomy of the hind flippers of two species of seals with reference to thermoregulation. Can. J. Zool. 48, 821–829.
- Thompson, S.D., Ono, K.A., Oftedal, O.T., Boness, D.J., 1987. Thermoregulation and resting metabolic rate of California sea lion (*Zalophus californianus*) pups. Physiol. Zool. 60, 730–736.
- Watts, P., Hansen, S., Lavigne, D.M., 1993. Models of heat loss by marine mammals: thermoregulation below the zone of irrelevance. J. Theor. Biol. 163, 505–525.
- Whittow, G.C., Ohata, C.A., Matsuura, D.T., 1971. Behavioral control of body temperature in the unrestrained California sea lion. Commun. Behav. Biol. 6, 87–91.
- Williams, T.M., 1999a. The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. Philos. Trans. R. Soc. Lond., Ser. B 354, 193–201.
- Williams, T.M., 1999b. Thermoregulation in adult female Steller sea lions and pups, Appendix B.13 of the Final Report of the Steller Sea Lion Physiology Workshop, Seattle, Washington, February 8–10, p. 34.
- Williams, T.M., Worthy, G.A.J., 2002. Anatomy and physiology: the challenge of aquatic living. In: Hoelzel, R. (Ed.), Marine Mammal Biology: An Evolutionary Approach. Blackwell Science, Oxford, pp. 73–97.
- Williams, T.M., Noren, D., Berry, P., Estes, J.A., Allison, C., Kirtland, J., 1999. The diving physiology of bottlenose dolphins (*Tursiops truncatus*): III. Thermoregulation at depth. J. Exp. Biol. 202, 2763–2769.
- Williams, T.M., Fuiman, L.A., Horning, M., Davis, R.W., 2004. The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddelli*: pricing by the stroke. J. Exp. Biol. 207, 973–982.
- Willis, K., 2004. Thermoregulation in Steller sea lions: an experimental approach. MS thesis. Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, 138 pp.
- Willis, K., Horning, M., Rosen, D.A.S., Trites, A.W., 2004. Spatial variation of heat flux in swimming Steller sea lions: evidence for consistent avenues of heat exchange along the body trunk. J. Exp. Mar. Biol. Ecol. 315, 163–175. ([doi:10.1016/j.jembe.2004.09.018](https://doi.org/10.1016/j.jembe.2004.09.018))
- Wissler, E.H., Ketch, R.B., 1982. Errors involved in using thermal flux transducers under various conditions. Undersea Biomed. Res. 9, 213–231.