

The effects of water temperature on the energetic costs of juvenile and adult California sea lions (*Zalophus californianus*): the importance of skeletal muscle thermogenesis for thermal balance

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SUMMARY

As highly mobile marine predators, many pinniped species routinely encounter a wide range of water temperatures during foraging and in association with seasonal, geographical and climatic changes. To determine how such variation in environmental temperature may impact energetic costs in otariids, we determined the thermal neutral zone of adult and juvenile California sea lions (*Zalophus californianus*) by measuring resting metabolic rate using open-flow respirometry. Five adult female (body mass range=82.2–107.2 kg) and four juvenile (body mass=26.2–36.5 kg) sea lions were examined over experimental water temperatures ranging from 0 to 20°C (adults) or 5 to 20°C (juveniles). The metabolic rate of adult sea lions averaged $6.4 \pm 0.64 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ when resting within the thermal neutral zone. The lower critical temperature of adults was $6.4 \pm 2.2^\circ\text{C}$, approximately 4°C lower than sea surface temperatures routinely encountered off coastal California. In comparison, juvenile sea lions did not demonstrate thermal neutrality within the range of water temperatures examined. Resting metabolic rate of the younger animals, $6.3 \pm 0.53 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$, increased as water temperature approached 12°C, and suggested a potential thermal limitation in the wild. To determine whether muscle thermogenesis during activity could mitigate this limitation, we measured the active metabolic rate of juveniles swimming at water temperature (T_{water})=5, 12 and 20°C. No significant difference ($F=0.377$, $P=0.583$) in swimming metabolic rate was found among water temperatures, suggesting that thermal disadvantages due to small body size in juvenile sea lions may be circumvented by recycling endogenous heat during locomotor activity.

Key words: thermal neutral zone, lower critical temperature, California sea lion, thermal substitution, swimming energetics.

INTRODUCTION

For endotherms, maintaining thermal balance is especially challenging when in water (Williams, 1983; Dejours, 1987; Hind and Gurney, 1997). The high thermal conductivity and heat capacity of water compared with air promotes elevated rates of heat loss through conductive and convective pathways. Consequently, marine endotherms have developed a variety of mechanisms to counteract excessive heat transfer when immersed. These include increased insulation (Scholander et al., 1950; Irving and Hart, 1957; Williams and Worthy, 2002), vascular specializations such as countercurrent heat exchange and peripheral vasoconstriction (Scholander and Schevill, 1955; Elsner, 1969; Irving, 1969; Tarasoff and Fisher, 1970; Pabst et al., 1999), elevated basal metabolic rates (Scholander et al., 1942; Williams et al., 2000) and increased metabolic heat production associated with the digestion of food (Costa and Kooyman, 1984; Yeates, 2006; Mostman Liwanag, 2008) and with locomotor activity (Williams, 1999).

Numerous studies have demonstrated elevated metabolic costs in aquatic and semi-aquatic mammals (Irving and Hart, 1957; Fish, 1979; Dawson and Fanning, 1981; Costa and Kooyman, 1982; Williams, 1986; Williams et al., 2001). While raising heat production through increased metabolism appears to be an effective mechanism by which to counteract heat loss, it also represents an added energetic expense to the animal, especially if employed over long periods. This problem can be exacerbated in young mammals, due both to

their small body size compared with adults and to an immature physiology. Smaller body size results in a larger surface area to volume ratio, such that the animal has proportionately more surface area through which heat can be transferred. In addition, physiological thermal capabilities are slow to develop in otariids (e.g. Donohue et al., 2000; Rutishauser et al., 2004). As a result, young otariids are more likely to experience thermoregulatory stress compared with adults.

The natural history of many species of pinnipeds requires independent living and foraging early in life (e.g. within days to one year) (Riedman, 1990). In view of the above, the thermal challenges encountered by these young animals are likely to be different from those of adults. For example, California sea lion (*Zalophus californianus*, Esson) pups wean between six and 12 months of age, at approximately one-third adult body mass (Heath, 1989). During the weaning process, pups do not learn foraging skills from their mothers (Melin et al., 2000); and the increased hunting time associated with learning to find food independently exposes young animals to extended periods of elevated heat loss. Depending on the duration and magnitude of these losses, the insulating blubber layer will be depleted as fat stores are converted to energy, resulting in a reduction of thermal stability in water and a spiraling decline in energy balance (Rutishauser et al., 2004; Rosen et al., 2007). Because thermoregulatory processes theoretically increase the costs of swimming and diving in pinnipeds (Hind and Gurney, 1997), the

thermal limitations of immature animals have the potential to impact the transition to the ocean and independent foraging.

In this study we investigated the thermal capabilities and limitations of one species of otariid, the California sea lion. The metabolic rates of both adult and juvenile sea lions resting over a range of water temperatures (T_{water}) were measured, and the results used to determine the thermal neutral zone (TNZ) for each life-history stage (Bartholomew, 1977). The TNZ was defined as the range of temperatures between the lower critical temperature (T_{LC}) and the upper critical temperature (T_{UC}). Outside of this temperature range, an animal must increase its metabolism (and thus energetic cost) to offset heat loss or facilitate heat dissipation, respectively.

As noted above, because immature animals are likely to experience greater thermal challenges than adults, we also examined one mechanism for mitigating potential thermal limitations in juvenile sea lions, the use of heat generated by swimming and diving to maintain core body temperature. An increase in metabolic heat production associated with swimming exercise has been demonstrated for pinnipeds and cetaceans (Williams, 1999). This elevated metabolic rate has been shown to provide thermal energetic benefits for a variety of aquatic and semi-aquatic mammals, including mink (Williams, 1983), muskrat (Fish, 1979) and the sea otter (Yeates et al., 2007). Here the importance of skeletal muscle thermogenesis for thermal balance in sea lions was evaluated by comparing the metabolic rates of juvenile animals resting and swimming in a flume at different T_{water} . By including colder T_{water} expected to be outside the TNZ, we were able to examine the effects of locomotor activity on total energetic responses.

MATERIALS AND METHODS

Animals

Nine California sea lions were used in this study (Table 1). Five adult females were housed at Long Marine Laboratory (Santa Cruz, CA, USA). Three of the adults were captive sea lions on loan from the Brookfield Zoo (Brookfield, IL, USA), and two were wild-caught from San Nicolas Island (CA, USA). Four juvenile (less than one year old) California sea lions (three males, one female), on loan from Sea World (San Diego, CA, USA), were housed at the Physiological Research Laboratory at Scripps Institution of Oceanography (La Jolla, CA, USA). All animals were maintained in saltwater pools and fed a daily diet of herring, capelin and/or mackerel supplemented with vitamins. T_{water} in the holding pools reflected ambient coastal water conditions and averaged 15°C for the adults and 18°C for the juveniles during the experimental period.

Experimental protocol

Adults

Oxygen consumption (\dot{V}_{O_2}) was determined by training the sea lions to rest quietly beneath a Plexiglas® metabolic hood (approximately 72 cm high × 40 cm wide × 138 cm long) mounted above a temperature-controlled saltwater pool. Animals were conditioned for several months prior to the tests to remain quiescent during the trials. T_{water} was arbitrarily varied between metabolic trials, from 0 to 20°C, in approximately 5°C increments. Temperature of the seawater was adjusted with ice or heated water, and was monitored throughout each trial to ensure that T_{water} remained constant ($\pm 1^\circ\text{C}$) over the course of the trial. Behavior of the animal was recorded continuously and only quiescent periods of at least 10 min were used in the analyses. Each experimental session consisted of a 5–10 min acclimation period at the trial T_{water} , followed by a 30–120 min data acquisition period under the metabolic dome. Each animal was tested only once per day, at a single experimental T_{water} ($\pm 1^\circ\text{C}$), and care was taken to avoid testing the same animal on sequential days. Resting \dot{V}_{O_2} was determined for 2–3 separate trials at each temperature for each animal. Rectal temperatures were recorded for the animals as described below.

Juveniles

\dot{V}_{O_2} and stomach temperature (T_{stomach}) were measured simultaneously as juvenile sea lions rested or swam at 1.0 m s⁻¹ against a current in a water channel (Hydraulics Laboratory, Scripps Institution of Oceanography, La Jolla, CA, USA). During swimming the animals were attached to a weighted line to create three work levels (25–50%, 75% and 80–100% of maximum effort). Loads were determined from the predicted metabolic scope of swimming sea lions (Feldkamp, 1987; Williams et al., 1991) and followed the procedures of di Prampero et al. (di Prampero et al., 1974). Exercise load was increased by adding weights to a line connected to a low-friction pulley system that was attached to a nylon loop carried on the back of the animal. Weights ranged from 1 to 5 kg depending on the animal, and were adjusted to submaximal exercise levels as determined in Williams et al. (Williams et al., 1991). The channel was filled with freshwater maintained at 5, 12 or 20°C. Additional details of the water channel and the experimental test section have been described in Davis et al. (Davis et al., 1985) and Williams et al. (Williams et al., 1991).

Four weeks prior to experimentation the sea lions were trained to swim consistently in the water channel at 1.0 m s⁻¹ for 20–30 min. No measurements for this study were made until reproducible values (within 5%) for \dot{V}_{O_2} were obtained. Each experimental session

Table 1. Body mass, resting metabolic rate and lower critical temperatures of the California sea lions used in this study

Animal	Body mass (kg) (means ± 1 s.d.)	Resting metabolic rate (ml O ₂ min ⁻¹ kg ⁻¹)	Lower critical temperature (°C)
Adult 1	99.8±1.9	6.16±0.79	5.3
Adult 2	82.2±0.9	7.13±0.70	5.1
Adult 3	95.3±1.2	6.88±0.23	5.4
Adult 4*	107.2±6.6	5.55±0.75	5.9
Adult 5*	88.8±1.5	6.10±0.49	10.4
Juv 1 (♂)	36.5±2.6	5.09±1.26	>12
Juv 2 (♂)	35.6±0.8	5.84±0.89	>12
Juv 3 (♂)	31.9±0.4	9.74±1.06	>12
Juv 4 (♀)	26.2±0.1	8.56±0.26	>12

Five adult female and four juvenile (three males, one female) California sea lions were examined. For the adults, wild-caught animals are indicated with asterisks. Body mass is the mean for the experimental period. Resting metabolic rate is the mean level measured within the thermal neutral zone for adults and the measurement at 20°C for juveniles. Lower critical temperatures for the adult animals were determined using segmented regression analysis (see text for details). The lower critical temperatures of juvenile animals probably occurred between 12 and 20°C.

consisted of a 20–60 min rest period followed by 20–30 min swim bouts at each of the three work loads. Swim bouts were separated by rest periods of at least 15 min. Resting values for \dot{V}_{O_2} and T_{stomach} were determined during 10 min quiescent periods before the swimming sessions as the animals floated in the water channel.

Oxygen consumption

The rate of \dot{V}_{O_2} during all trials was measured by open-flow respirometry following the protocols of Williams et al. (Williams et al., 2002). Adult sea lions were fasted overnight (≥ 12 h). Conditions for basal metabolic rate (BMR) were followed for the adults, such that animals were non-pregnant, non-lactating, post-absorptive and sedentary (Kleiber, 1975). Ambient air was drawn through the Plexiglas chamber at 1551 min^{-1} , with flow rates maintained and monitored continuously with a mass flow controller (Flowkit 500, Sable Systems International, Las Vegas, NV, USA). Samples of air from the exhaust port of the chamber were dried (Drierite; W. A. Hammond Drierite Co., Xenia, OH, USA) and scrubbed of CO_2 (Sodasorb; Chemetron, St Louis, MO, USA) before entering an oxygen analyzer (FC-1, Sable Systems). The percentage of O_2 in the expired air was monitored continuously and recorded once per second with a personal computer using Sable Systems software. \dot{V}_{O_2} was then calculated using equation 4b from Withers (Withers, 1977) and an assumed respiratory quotient of 0.77 (Feldkamp, 1987; Boyd et al., 1995; Arnould et al., 2001). All values were corrected to STPD. The lowest continuous \dot{V}_{O_2} that was maintained for 10–20 min and corresponded to quiescent behavior was used for the analyses. The entire system was calibrated daily with dry ambient air (20.94% O_2) and every 3–4 days with dry span gases (16.0% O_2) and N_2 gas according to Fedak et al. (Fedak et al., 1981). The theoretical fraction of O_2 leaving the chamber was calculated from Davis et al. (Davis et al., 1985) and compared with measured values from the analyzer.

\dot{V}_{O_2} measurement methods for the juvenile sea lions were similar to those used for the adults, with the following differences. \dot{V}_{O_2} measurements were performed with animals resting or swimming in a flume. Details of the system have been reported previously (Davis et al., 1985; Williams et al., 1991). Briefly, the sea lions swam in a glass paneled test section that was 2.5 m long and had a cross-sectional area of 1.1 m^2 . A plywood cover restricted breathing in the test section to a 1.1 m long \times 0.6 m wide \times 0.3 m high Plexiglas skylight dome. Ambient air was drawn into the dome at approximately $80\text{--}90 \text{ min}^{-1}$ (100 Flo-Sen; McMillan Co., Georgetown, TX, USA). Flow rates were adjusted to ensure an O_2 content in the dome in excess of 20% over 1 min intervals. Samples of the outflow of the metabolic dome were dried (Drierite) and scrubbed of CO_2 (Baralyme, Allied Healthcare Products, St Louis, MO, USA) before entering an oxygen analyzer (Ametek S3-A, Paoli, PA, USA). Voltage output of the analyzer was monitored by an A/D converter (Keithley 500, Cleveland, OH, USA) connected to a personal computer. Calculations and calibrations were as described above for the adult measurements. The respirometry system used for the juveniles was cross-calibrated with that used for the adults by running both systems simultaneously (Williams et al., 2004). As with the adults, juvenile sea lions were fasted (≥ 12 h) prior to each metabolic trial, and were not fed until after measurements were complete for that trial.

Core temperature

Core temperature of the animals was monitored to assess heat storage or loss across T_{water} . Rectal temperature of the adult sea lions was measured before and after metabolic trials with a flexible

thermocouple probe (RET-1, Physitemp Instruments, Inc., Clifton, NJ, USA) inserted approximately 20 cm into the rectum. Values were recorded ($\pm 0.1^\circ\text{C}$) from a digital thermometer (BAT-12, Physitemp Instruments, Inc.). For the juveniles, core body temperature was determined from T_{stomach} during rest and swimming, as this method allowed for core temperature to be monitored in active animals. T_{stomach} was monitored continuously with an ingested temperature-sensitive radio transmitter pill (Model L-M; Mini-Mitter, Inc., Bend, OR, USA). Prior to use, each pill was calibrated in a temperature-controlled bath over a range of $32\text{--}42^\circ\text{C}$. Calibrated pills were then fed to each sea lion in a fish, at least 12 h prior to any metabolic measurements. During metabolic trials, pulse signals from the pills were received on a handheld radio receiver (Realistic Model CH-3; Radio Shack, Fort Worth, TX, USA) and averaged for 1 min intervals for every 5 min of rest or exercise. Rectal temperature of the juvenile sea lions was also measured before and after each experimental period using a thermocouple probe and digital thermometer (Physitemp Instruments, Inc.). These values were compared with T_{stomach} and used to assess stability of the temperature pills by generating a regression between rectal temperatures and T_{stomach} pulse signals for each animal ($R^2 > 0.99$ for each). To avoid drift after calibration, individual pills were used for less than 10 consecutive days during the experimental period.

Statistical analyses and calculations

Values for \dot{V}_{O_2} for adult sea lions are presented as means ± 1 s.d. To determine the T_{LC} of each adult sea lion, a breakpoint for the relationship between mass-specific resting metabolic rate (RMR) and T_{water} was defined from a segmented regression analysis minimizing the sum of the residual sum of squares (Sokal and Rohlf, 1981; Nickerson et al., 1989; Williams et al., 2001). The temperature at which the two lines of best fit intersected was used to define the T_{LC} . The T_{LC} was determined by this method for each individual sea lion (Table 1). Differences between rectal temperatures before and after metabolic trials were determined by a randomized block design, with individuals as blocks (Systat 10.2, Systat Software, Chicago, IL, USA). Linear regressions of rectal temperatures with T_{water} were calculated by least-squares procedures (Zar, 1974).

For the juvenile sea lions values for both \dot{V}_{O_2} and T_{stomach} are presented as means ± 1 s.d. Differences among RMRs at different T_{water} were determined by one-way analysis of variance (ANOVA) using a Bonferroni pairwise multiple comparison test (Systat). Differences among swimming metabolic rates at different T_{water} were determined by repeated-measures ANOVA (Systat). Linear relationships were calculated by least-squares procedures (Zar, 1974).

Theoretical swimming velocities for juvenile sea lions were calculated from load values, following the methods of Williams et al. (Williams et al., 1991). Briefly, each load was converted into a drag force (Newtons) by multiplying the load mass (kg) by the acceleration due to gravity (9.8 m s^{-2}). This value was added to a calculated value for body drag, based on parameters measured for California sea lions according to:

$$\text{Drag} = \frac{1}{2} \rho v^2 A C_D, \quad (1)$$

where ρ is the density of water (10 kg m^{-3}), v is forward velocity (1 m s^{-1}), A is the surface area of the sea lion calculated from a mass-based regression using data from Feldkamp (Feldkamp, 1987) and C_D is the drag coefficient (0.004067) averaged from Feldkamp (Feldkamp, 1987). Theoretical swimming velocity was calculated for each added load by solving the drag equation for v , to find the

velocity necessary to overcome the calculated total drag force. Measured metabolic rates ($\text{ml O}_2 \text{kg}^{-1} \text{min}^{-1}$) were converted to Watts (J s^{-1}), assuming a mean caloric equivalent of $20.1 \text{ kJ l}^{-1} \text{ O}_2$ (Schmidt-Nielsen, 1997). Exponential relationships for $\dot{V}\text{O}_2$ in relation to swimming velocity were calculated by least-squares procedures (Zar, 1974).

RESULTS

Resting metabolism and thermal neutral zone

T_{LC} was determined for each individual adult sea lion by a rise in RMR (Table 1). The mean T_{LC} for the adult sea lions was $6.4 \pm 2.2^\circ\text{C}$ (Fig. 1A). This indicated a TNZ of at least 16°C , as metabolic rate did not change significantly between 6.4°C and 22.4°C ($F=3.429$, $P=0.072$). The mean metabolic rate (RMR) of adult California sea lions resting in water within the TNZ was $6.4 \pm 0.64 \text{ ml O}_2 \text{kg}^{-1} \text{min}^{-1}$. Below the TNZ, resting metabolism increased to a maximum of $10.2 \pm 1.73 \text{ ml O}_2 \text{kg}^{-1} \text{min}^{-1}$ at $0.9 \pm 0.5^\circ\text{C}$. At the coldest temperatures, individual sea lions experienced a 30–94% increase in RMR above their respective means within the TNZ. The mean linear increase in RMR below the TNZ (Fig. 1A) was described by the equation:

$$\text{RMR} = 10.80 - 0.63 (T_{\text{water}}), \quad (2)$$

where RMR is in $\text{ml O}_2 \text{kg}^{-1} \text{min}^{-1}$ and T_{water} is in $^\circ\text{C}$ ($P < 0.0001$, $R^2 = 0.34$).

The metabolic rate of juvenile California sea lions resting in water ranged from 6.3 ± 0.53 to $8.7 \pm 0.52 \text{ ml O}_2 \text{kg}^{-1} \text{min}^{-1}$ and was

dependent on T_{water} . Resting metabolism of the animals increased significantly ($N=12$, $F=23.432$, $P=0.001$) as T_{water} decreased over the range of $5\text{--}20^\circ\text{C}$ (Fig. 1B) and was described by the equation:

$$\text{RMR} = 9.59 - 0.16 (T_{\text{water}}), \quad (3)$$

where RMR is in $\text{ml O}_2 \text{kg}^{-1} \text{min}^{-1}$ and T_{water} is in $^\circ\text{C}$ ($P=0.001$, $R^2=0.67$). Resting metabolism did not differ significantly between 5 and 12°C ($P=0.29$) or 12 and 20°C ($P=0.068$) but did differ significantly between 5 and 20°C ($P=0.004$). Individual sea lions demonstrated a 26–68% increase in RMR over the 15°C decrease in T_{water} . Mean metabolic rate at $T_{\text{water}}=20^\circ\text{C}$ was $6.3 \pm 0.53 \text{ ml O}_2 \text{kg}^{-1} \text{min}^{-1}$ and was comparable with that reported by Feldkamp (Feldkamp, 1987) for sea lions resting at similar acclimation temperatures. The mean RMR for the juveniles at 20°C was similar to that of the adults within their TNZ (Table 1). However, the two smallest juveniles exhibited significantly higher RMR values than the adults or larger juveniles ($P=0.03$; Table 1).

Core temperature

Resting adult sea lions maintained rectal temperatures between 35.8 and 38.2°C (mean= $37.0 \pm 0.5^\circ\text{C}$) during the metabolic trials (Fig. 1C). There was no significant difference between pre-trial and post-trial rectal temperatures for any sea lion ($F=0.35$, $P=0.56$), although rectal temperature did differ among individuals ($F=16.14$, $P < 0.001$). Post-trial rectal temperature was not significantly correlated with experimental T_{water} ($F=0.76$, $P=0.39$; Fig. 1C).

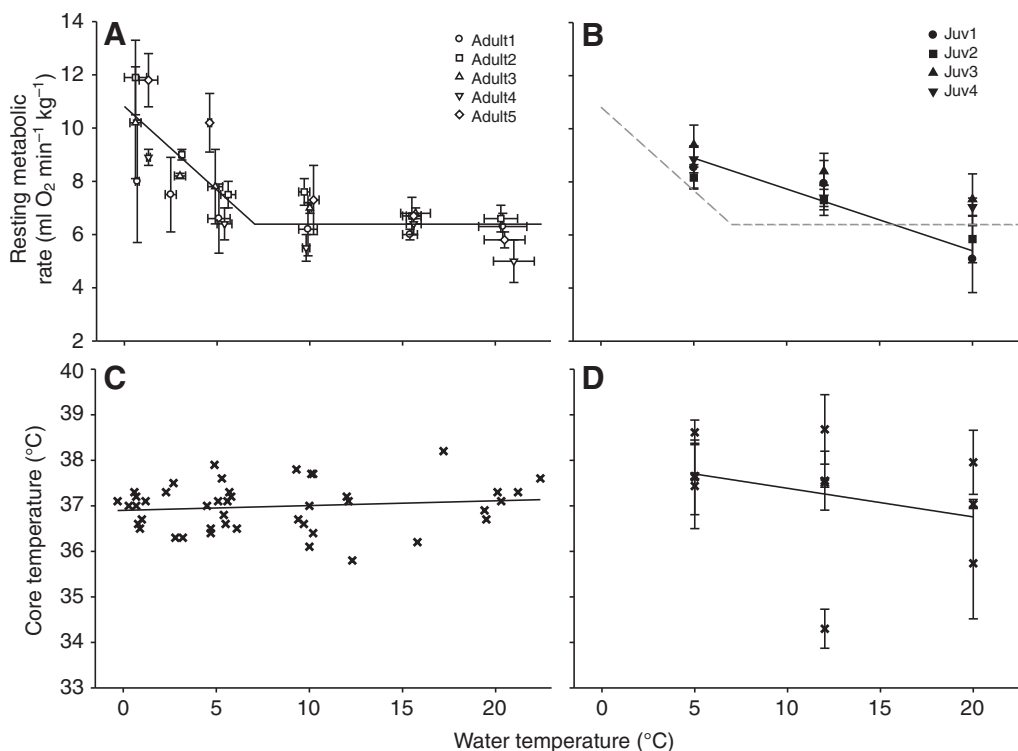


Fig. 1. Resting metabolism and core body temperature in relation to water temperatures for adult (A,C) and juvenile (B,D) California sea lions. In (A) each point represents the mean of 2–3 independent trials for the same animal at similar temperatures, with error bars indicating ± 1 s.d. Lines represent the mean results of segmented regression analysis and are presented in the text. The temperature at the breakpoint between the two lines indicates the lower critical temperature for adult sea lions. In (B) each point represents a single independent trial for each juvenile sea lion, with error bars indicating ± 1 s.d. for individual temperatures. The solid line represents the best-fit linear regression for the data and is described in the text. The broken line represents the mean results for adult female California sea lions, for comparison. Core body temperature for adult (C) and juvenile (D) sea lions was measured immediately following or during each metabolic trial, respectively. Points in C represent individual post-trial measurements; in D mean values ± 1 s.d. for each trial are represented by points and error bars. The outlying body temperature at water temperature ($T_{\text{water}}=12^\circ\text{C}$) in D is for Juv2 (see Table 1). Each line denotes the least-squares linear regression as described in the text.

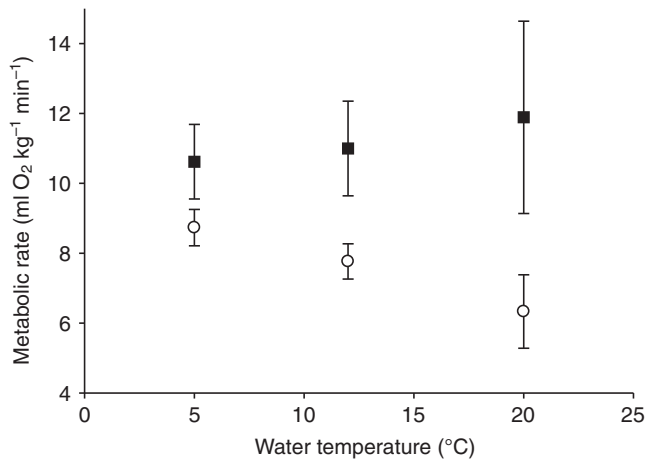


Fig. 2. Metabolic rate in relation to water temperature for juvenile California sea lions at rest (white circles) and while swimming at 1 m s^{-1} (black squares). Symbols and lines indicate mean values ± 1 s.d. Note that resting metabolic rate decreased with increasing water temperature whereas swimming metabolic rate did not differ significantly among the water temperatures.

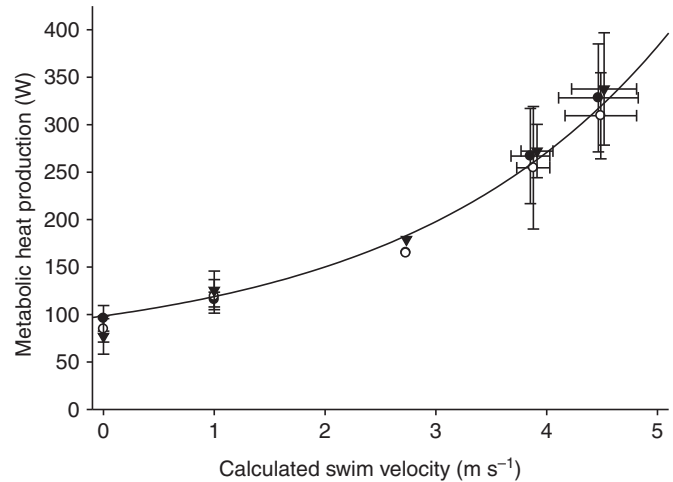


Fig. 3. Metabolic heat production in relation to calculated swim velocity for four juvenile California sea lions. Three water temperatures are included: 5°C (closed circles), 12°C (open circles) and 20°C (downward facing triangles). Points represent mean values ± 1 s.d. (error bars) or single measurements (no error bars). The line represents the least-squares exponential relationship through the data points for swimming metabolism and is described in the text.

Whether resting or swimming, all juvenile sea lions maintained T_{stomach} between 34 and 40°C . Rectal temperatures (used for stomach temperature pill calibrations) ranged from 34.2 to 37.3°C . Mean T_{stomach} for the juvenile animals resting in the water channel was $37.3 \pm 1.3^\circ\text{C}$ ($N=11$) for T_{water} ranging from 5 to 20°C (Fig. 1D). T_{stomach} was not significantly correlated with experimental T_{water} during rest or swimming ($F=0.956$, $P=0.354$). Swimming activity had no consistent effect on T_{stomach} of the juvenile sea lions. Mean T_{stomach} following 20 min of swimming at 1 m s^{-1} with no load was $37.8 \pm 0.1^\circ\text{C}$ at $T_{\text{water}}=5^\circ\text{C}$, $38.0 \pm 0.7^\circ\text{C}$ at 12°C and $36.7 \pm 0.6^\circ\text{C}$ at 20°C . T_{stomach} for sea lions swimming with maximum loads was within 0.9°C of these values at comparable T_{water} .

Activity thermogenesis

The swimming metabolism of juvenile sea lions was independent of T_{water} (Fig. 2) over the range of exercise loads examined (Fig. 3). Thus, no statistical difference in metabolic rate was apparent among the three T_{water} examined when swimming at 1 m s^{-1} only or swimming at this speed with additional loads of 3 kg or $4\text{--}5 \text{ kg}$ (repeated-measures ANOVA, $N=3$, $F=0.337$, $P=0.583$). Mean \dot{V}_{O_2} for sea lions swimming freely at 1 m s^{-1} (i.e. with no load) was $11.17 \pm 0.36 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ for all three T_{water} . This value was within 10% of that reported by Feldkamp (Feldkamp, 1987) and Williams et al. (Williams et al., 1991) for similarly sized sea lions swimming at the same speed at $T_{\text{water}}=15\text{--}18^\circ\text{C}$.

Swimming metabolic heat production (Watts) of the sea lions increased exponentially with calculated velocity (Fig. 3) and was described by the equation:

$$\text{MR} = 59.85 + 38.65e^{0.4244v}, \quad (4)$$

for all four sea lions exercising across all T_{water} , where v is in m s^{-1} ($P<0.0001$, $R^2=0.86$). This non-linear pattern in energetic cost would be expected due to the exponential increase in hydrodynamic drag with increases in swimming velocity (Feldkamp, 1987).

DISCUSSION

Thermal capabilities of the California sea lion

Based on the width of the TNZ and the T_{LC} values identified for adult California sea lions in the present study, this otariid species shows remarkable thermal tolerance over a wide range of temperatures (Fig. 1A,C), despite a relatively thin blubber layer (Mostman Liwanag, 2008). The T_{LC} values measured for adult female sea lions indicate that this age class does not incur additional thermoregulatory energetic costs in the routine water temperatures encountered off the California coast, even while resting. The mean T_{LC} for adults, $6.4 \pm 2.2^\circ\text{C}$ (Fig. 1A), is approximately 4°C lower than the range of sea surface temperatures encountered by this species and age class (Rice, 1998; Reeves et al., 2002) (NASA MODIS database, <http://modis.gsfc.nasa.gov/>). Compared with other temperate marine mammals, including the sea otter, *Enhydra lutris* (Morrison et al., 1974; Costa and Kooyman, 1984), harbor seal, *Phoca vitulina* (Hart and Irving, 1959) and bottlenose dolphin, *Tursiops truncatus* (Costa and Williams, 1999), the California sea lion has a relatively wide TNZ of at least 16°C , and thus a large thermal territory available for foraging and movement. Such thermal flexibility probably also allows for continued range expansion and consequent tolerance to climatic changes. Admittedly, lower water temperatures will be encountered as the sea lions move below the thermocline during diving. However, both the relatively short duration of dives (Feldkamp et al., 1989) and the potential for increased heat production through skeletal muscle thermogenesis (see below) may circumvent any thermal energetic disadvantages associated with lower water temperatures at depth.

To maintain energy balance, California sea lions, like many other species of marine mammals, must balance the benefits of a large geographical range with potential energetic disadvantages that occur when thermal limits are exceeded. The specific temperature ranges depend on species and relative thermal capabilities. Thus, a relationship between T_{LC} and oceanic movements exists for phocid seals, such that species occupy, and may be limited to, ranges that

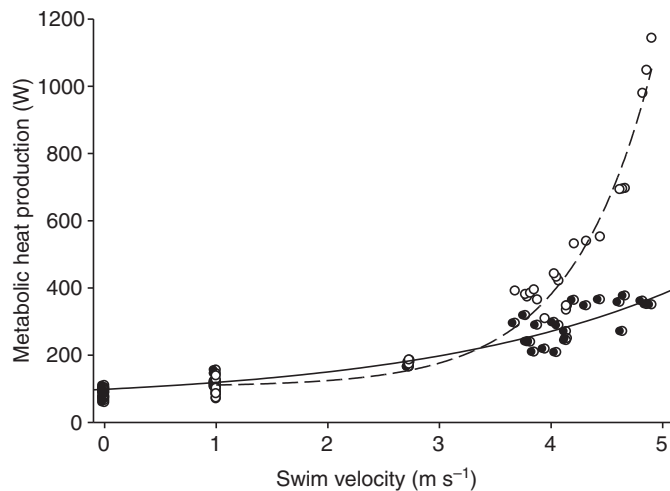


Fig. 4. Comparison of predicted (open circles) and measured (closed circles) metabolic heat production in relation to calculated swim velocity for juvenile sea lions. Predicted rates are based on the model proposed by Hind and Gurney (Hind and Gurney, 1997). The solid line is the least-squares exponential relationship for measured swimming metabolism as described in the text; the broken line is the least-squares exponential relationship for the predicted swimming metabolism of the animals.

enable them to maintain minimum resting metabolic rates in the wild (Hart and Irving, 1959; Gallivan and Ronald, 1979). With a T_{LC} below 0°C , harp seals (*Phoca groenlandica*) can maintain basal metabolic rates at temperatures several degrees below environmental temperatures (Gallivan and Ronald, 1979) whereas harbor seals alter movements seasonally to remain in water temperatures close to their exact T_{LC} (Hart and Irving, 1959). In comparison, California sea lions range from Washington to Mexico (adult females: California to Mexico), where sea surface temperatures can range from approximately 5 to 30°C (female range: 10 – 30°C) (Rice, 1998; Reeves et al., 2002) (NASA MODIS database).

California sea lions may increase their geographical range of movements by utilizing vascular control to improve body insulation when acutely exposed to cold water (Elsner, 1969; Irving, 1969; Elsner, 1999). We found that individual variability in RMR increased as water temperatures decreased below the T_{LC} (Fig. 1A). Such a response may be due to modifications in the level of perfusion and concomitant thermal conductance of the insulating blubber layer. Such vascular modifications have been observed for phocid seals, which use a dynamic insulating blubber layer as means for heat conservation or dissipation, even along the well-insulated trunk region (Mauck et al., 2003). It is possible that the variability in metabolism below the T_{LC} observed in the present study for California sea lions reflects variability in the level of perfusion across the blubber layer, a hypothesis that warrants further investigation.

Thermal limitations in juvenile sea lions

During the transition to independence, young pinnipeds theoretically have access to the same oceanic foraging grounds as adult conspecifics. However, the thermal energetic costs associated with immersion are greater in smaller, immature animals compared with adults and may limit the range for foraging by juveniles at a critical point in their life history. The implications for young phocids and otariids are likely to be quite different due to differences in their insulation. Young phocids have a significantly thicker and better quality (higher lipid content) blubber layer compared with young

otariids (Mostman Liwanag, 2008). Accordingly, juvenile harp seals and harbor seals appear to be thermally competent in the range of water temperatures often encountered by adults in the wild (Hart and Irving, 1959; Gallivan and Ronald, 1979). This contrasts with young otariids, which appear to exhibit reduced thermal capabilities (compared with adults) during the period of transition to independent living. Both pup and juvenile Antarctic fur seals (*Arctocephalus gazella*) demonstrate elevated thermal energetic costs that limit the range of foraging and prevent these age classes from accessing adult foraging grounds (Rutishauser et al., 2004). Northern fur seal (*Callorhinus ursinus*) pups also show elevated metabolic rates at water temperatures regularly encountered in the wild, even in coastal regions close to the rookery (Donohue et al., 2000; Mostman Liwanag, 2008).

A major consequence of the metabolic responses of juvenile California sea lions compared with adults is the potential effect on resting at sea. For the juveniles in this study, rest periods were the most thermally challenging, and were associated with an increase in metabolic rate as T_{water} decreased (Fig. 1B). With no clear TNZ between 5 and 20°C , juvenile California sea lions probably experience added energetic costs when resting within their natural range of water temperatures. Although RMR at 20°C was significantly higher in the two smaller juveniles ($9.15 \pm 0.83 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$) compared with the larger juveniles ($5.47 \pm 0.53 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$), all four animals exhibited increases in metabolism at 12°C (Fig. 1B). This marked difference in mass-specific metabolism may represent a body-size threshold for RMR between 32 and 35 kg (Table 1).

The effect of locomotor activity on thermal responses in juvenile sea lions

One important potential mechanism to offset the thermal limitations experienced by juvenile California sea lions at sea is utilization of heat generated by swimming. Thermal benefits associated with skeletal muscle thermogenesis depend on the balance between elevated heat loss associated with convective cooling and increased heat production that occurs with locomotor activity by the swimmer (Hind and Gurney, 1997). Although sea lions represent one of the larger aquatic species examined, the concept of thermal substitution of heat produced by exercise is not new, and has been demonstrated in several species of aquatic birds and rodents (reviewed by Lovvorn, 2007).

Hind and Gurney modeled the metabolic cost of swimming in several marine mammal species, including juvenile California sea lions (Hind and Gurney, 1997). Their model accounted for both hydrodynamic and thermal interactions between the animals and the surrounding water. By incorporating our measured values for RMR above and below the T_{LC} into the Hind and Gurney (Hind and Gurney, 1997) model, we were able to compare their thermal predictions with the measured heat production at different swimming velocities (Fig. 4). While our data and the model predictions agree at velocities up to 3 m s^{-1} , large differences occur at higher swimming velocities. Above 3 m s^{-1} , the model markedly overestimates metabolic heat production. Although most sea lions do not routinely maintain such high swimming velocities, this difference does suggest the use of physiological mechanisms to moderate energy expenditure at elevated exercise intensities.

One explanation for the difference between predicted and measured swimming metabolism may be the dynamic nature of body temperature control in these animals. While the Hind and Gurney (Hind and Gurney, 1997) model accounts for higher rates of heat loss through the blubber at greater swim speeds, it also allows

blubber conductivity to increase indefinitely, potentially resulting in conductivity values across the blubber that exceed actual rates of heat loss. In addition, otariids exhibit highly dynamic control over the vasculature across the blubber and the skin, enabling substantial changes in heat flow across the insulation over short time scales (Boyd, 2000; Willis et al., 2005). As a consequence, a purely physical model may not be sensitive enough to fully account for such behavioral adjustments of heat flow.

We found that activity served an important role for maintaining thermal energetic balance in young sea lions. When resting, juvenile sea lions demonstrated an increase in metabolism with declining water temperatures below 20°C (Fig. 1B). With swimming activity and the skeletal muscle thermogenesis associated with flipper movements, this change in metabolism was mitigated (Fig. 2).

In mammals, the conversion of stored energy into mechanical energy during exercise is relatively inefficient, and approximately 80% of the energy is converted into heat (Hodgson et al., 1994). Juvenile sea lions appear to use this heat to offset elevated thermal demands at low water temperatures, as we found that water temperature (over the range of 5–20°C) had no effect on metabolic rate during swimming regardless of exercise load (Fig. 3). Rather than being additive, increased heat production associated with activity counterbalanced the increased thermal demands associated with lower water temperatures. Interestingly, this metabolic compensation occurred at relatively low levels of effort. Swimming speeds as low as 1 ms⁻¹, approximately 66% of the routine surface speed of free-ranging adult sea lions (Ponganis et al., 1990), resulted in sufficient heat to compensate for the thermal demands associated with a 15°C decrease in T_{water} (Fig. 2). By remaining active when at sea, young sea lions can probably avoid prolonged energetic thermal demands that would otherwise occur when resting in water below their T_{LC} . Although affording the ability to forage over a larger range, the disadvantage of this compensation strategy over the long term will ultimately be an increase in energetic cost due to activity, at least relative to adults (Fig. 1).

In summary, relatively low levels of swimming activity effectively compensated for the elevated thermoregulatory demands experienced at lower water temperatures in juvenile sea lions, probably by enabling the use of heat generated by skeletal muscle activity to meet thermal energetic demands. This occurred even at relatively low levels of activity. At high levels of activity, juvenile sea lions exhibited metabolic rates lower than predicted by hydrodynamic and thermal models. Both adult and juvenile sea lions may potentially exercise a high level of physiological control over their insulation, presumably by cardiovascular mechanisms, and this would probably allow energetic costs to be minimized over a wide range of water temperatures and activity levels. Together, the wide range of thermal tolerances exhibited by adult California sea lions and the ability of juvenile sea lions to utilize the heat produced by exercise enables this species both to occupy habitats with water temperatures below its TNZ and to respond rapidly to changes in environmental water temperatures.

LIST OF ABBREVIATIONS

A	surface area
BMR	basal metabolic rate
C_D	drag coefficient
TNZ	thermal neutral zone
T_{LC}	lower critical temperature (°C)
T_{UC}	upper critical temperature (°C)
T_{stomach}	stomach temperature (°C)
T_{water}	water temperature (°C)

\dot{V}_{O_2}	rate of oxygen consumption (ml O ₂ kg ⁻¹ min ⁻¹)
RMR	resting metabolic rate (ml O ₂ kg ⁻¹ min ⁻¹)
v	forward velocity
ρ	density of H ₂ O

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