

SHORT COMMUNICATION

Maintaining control: metabolism of molting Arctic seals in water and when hauled out

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ABSTRACT

Seals haul out of water for extended periods during the annual molt, when they shed and regrow their pelage. This behavior is believed to limit heat loss to the environment given increased peripheral blood flow to support tissue regeneration. The degree to which time in water, particularly during the molt, may affect thermoregulatory costs is poorly understood. We measured the resting metabolism of three spotted seals (*Phoca largha*), one ringed seal (*Pusa hispida*) and one bearded seal (*Erignathus barbatus*) during and outside the molting period, while resting in water and when hauled out. Metabolic rates were elevated in spotted and ringed seals during molt, but comparable in water and air for individuals of all species, regardless of molt status. Our data indicate that elevated metabolism during molt primarily reflects the cost of tissue regeneration, while increased haul out behavior is driven by the need to maintain elevated skin temperatures to support tissue regeneration.

KEY WORDS: Energetics, Thermoregulation, Molting physiology, Respirometry

INTRODUCTION

Whether marine mammals have higher baseline metabolic rates than their terrestrial counterparts has been debated for decades (Lavigne et al., 1986), although available data suggest that the various marine mammal lineages exhibit differing metabolic patterns (Costa and Maresh, 2017). One long-standing argument suggests that marine mammals should have higher innate thermoregulatory costs (e.g. Irving and Hart, 1957; Kanwisher and Ridgway, 1983; South et al., 1976) given that heat conduction in water is 24 times greater than in air at the same temperature (Dejours, 1987). The effect of medium (air versus water) on metabolism cannot be readily tested with fully aquatic marine mammals (cetaceans and sirenians). However, amphibious marine mammals (phocids, otariids, odobenids) provide an opportunity to examine this issue, as pinnipeds must thermoregulate in water, on land and sometimes upon ice. If submergence in water poses additional thermal costs, then resting metabolism for these species should be greater when in water

compared with when individuals are hauled out in air. However, the existence of physiological adaptations to prevent heat loss in water, including extensive insulation and ability to control peripheral blood circulation via arteriovenous anastomoses (Favilla and Costa, 2020), would argue against such a difference. Limited data are available to clarify these issues (Donohue et al., 2000; Hart and Irving, 1959; Irving and Hart, 1957; Noren, 2002; Pearson et al., 2022) and are confounded by differences in the species, age or sex of study animals, or in the timing of metabolic measurements.

Seasonal timing of data collection is especially important as individuals may have different thermoregulatory capacities, strategies, or constraints at different times of year owing to changes in body condition, energetic priorities and related physiology. For example, the consequences of differential thermal costs related to specific surrounding media may become more acute during the annual molt, when pinnipeds replace their pelage and several layers of skin. During this time, individuals typically haul out of water for extended periods, and warm their skin through increased peripheral blood flow (Paterson et al., 2012; Walcott et al., 2020). Previous studies have shown that resting metabolism is typically elevated for phocid seals during the molt (Boily, 1996; Boily and Lavigne, 1997; Chabot and Stenson, 2002; Hedd et al., 1997; Renouf and Gales, 1994; Thometz et al., 2021; Williams et al., 2011), most likely because of the direct cost of pelage replacement, the requirement to raise body surface temperatures to facilitate tissue regrowth or some combination of the two. Minimizing time in water is often interpreted as a strategy to limit the energetic cost of molt by reducing potentially high rates of heat loss in aquatic environments during the interval of increased peripheral perfusion (Boily, 1995). However, if seals employ active physiological adaptations, such as modulation of peripheral blood flow, then uncontrolled heat loss would be prevented when a molting seal needed to enter the water. If true, this would imply that increased haul out behavior during the molt is primarily related to the controlled maintenance of elevated skin temperatures and not the need to limit uncontrolled thermal costs.

Regardless of the primary driver of seasonal changes in haul out behavior, circumstances that increase time in water during the molt could impose additional thermoregulatory costs, extend the molting period and/or prevent a successful molt, as skin temperatures must reach certain thresholds for tissue regeneration to occur (Feltz and Fay, 1966). These considerations are particularly relevant for ice-associated seals. Arctic and sub-Arctic seals inhabit cold, polar waters that would magnify metabolic consequences related to conductive heat loss. Furthermore, these seals are experiencing rapid environmental changes due to global warming (Kovacs et al., 2011; Laidre et al., 2008, 2015). Reduced availability of sea ice platforms as appropriate haul out substrate will likely influence the amount of time seals spend out of water. Also, increasing human activity in the Arctic may contribute to instances of anthropogenic disturbance that force animals to alter routine behavior, resulting in

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additional time spent in water. Understanding how submersion in water affects Arctic seal metabolism both during and outside the molting period can provide valuable information about the continuing impacts of Arctic warming, sea ice loss and disturbance. In addition, such information should help to clarify outstanding questions regarding the impact of aquatic living on the metabolism of marine mammals.

Here, we measured the resting metabolic rate (RMR) of individual spotted, ringed and bearded seals, under controlled conditions while they were resting calmly in water and when hauled out in air, both during and outside their regular molting period. The goal was to determine if there was a difference in metabolism associated with the surrounding medium and how this relationship was influenced by the molting status of these ice-associated seals.

MATERIALS AND METHODS

Study animals

Three spotted seals (*Phoca largha* Pallas 1811) and one ringed seal [*Pusa hispida* (Schreber 1775)] at the Alaska SeaLife Center (Seward, AK, USA) and one bearded seal (*Erignathus barbatus* Erxleben 1777) at Long Marine Laboratory (Santa Cruz, CA, USA) participated in metabolic measurements across a 3-year period (2019–2021). The animals ranged in age from 4 to 11 years. They were considered sexually mature adults with the exception of one spotted seal that was a subadult during the first season (Table 1). Seals were maintained within established animal care programs since they were less than 1 year old. All individuals were in good long-term health. Each seal was offered a daily diet of freshly thawed fish and cephalopods with appropriate vitamin supplementation; food intake and body mass were allowed to fluctuate naturally based on behavioral indicators of appetite and motivation (Rosen et al., 2021). Body mass was recorded weekly to ± 0.1 kg using a calibrated platform scale.

The seals lived in outdoor enclosures with saltwater pools surrounded by dry resting areas. Ambient air and water temperatures were monitored hourly using TidBit v2 temperature data loggers (Onset Computer Corporation, Bourne, MA, USA). At the Alaska SeaLife Center, water temperatures during data collection were 4.5–7.8°C and air temperatures were 7.2–20.4°C. At Long Marine Laboratory, water temperatures were 9.5–12.8°C and air temperatures were 14–24.1°C.

Metabolic measurements were obtained from cooperating seals using positively conditioned behavior established through incremental operant conditioning. Although this voluntary behavioral control required substantial training investment, this strategy allowed

individuals to refuse participation or exit metabolic enclosures at any time, which minimized potential stress during data collection. In addition to metabolic sampling, the spotted and ringed seals participated in related physiological sampling including opportunistic monitoring of skin surface temperatures using both serial thermal imaging and direct measurement of subdermal skin temperatures following haul out (Fig. S1). Animal protocols were reviewed and approved by the Institutional Animal Care and Use Committee (IACUC) at the University of California Santa Cruz with cooperation from the IACUC at the Alaska SeaLife Center. Research was authorized by the United States National Marine Fisheries Service (Marine mammal research permit 18902) with expressed support from the Ice Seal Committee, a tribally authorized Alaska Native co-management organization.

Study design

Given that the resting metabolism of Arctic seals changes during the year (Thometz et al., 2021), this study was designed to use ‘paired’ measurements of RMR from individuals in water and in air. Matching in-air and in-water metabolic measurements were obtained within 48 h of each other to limit the influence of time on observed patterns and to ensure an equal number of in-air and in-water data points for each individual. Data collection occurred during the duration of the visible molt (molting condition) as well as within the 2 months before and after the visible molting period (non-molting condition). We aimed to collect paired measurements from each seal 1–2 times each month, depending on the behavioral tolerance of each seal. Not all data collection attempts resulted in successful completion of paired in-air and in-water data points; non-paired data were excluded from the analysis.

Prior to metabolic measurements, seals were fasted overnight for at least 12 h to ensure a post-absorptive state. Each seal was trained to voluntarily enter two metabolic chamber types: one rectangular chamber positioned on land near the seal’s living enclosure and one domed enclosure floating on the water’s surface. Often, seals were already in the medium (i.e. air or water) in which they were being measured prior to the initiation of data collection; however, this was not always the case. We attempted to impose minimum acclimation periods, but given the completely voluntary nature of data collection and differing preferred states, this varied from a few minutes to several hours (Table S1). Within both chamber types, seals were conditioned to rest calmly while rate of oxygen consumption was measured. The behavior of a seal was continuously evaluated in real time. In addition to resting calmly, behavioral criteria included

Table 1. Subject data for seals including annual timing of molt

Species	Seal ID	Sex	Site	Age (years)	Year	Start of molt	Peak (50%) molt	End of molt	Molt duration (days)
Spotted seal (<i>Phoca largha</i>)	Tunu	Male	AK	9	2019	23 May	12 June	19 June	28
				11	2021	18 May	10 June	14 June	28
	Sura	Female	AK	5	2019	29 April	14 May	22 May	24
				6	2020	27 April	18 May	27 May	31
				7	2021	3 May	18 May	25 May	23
	Kunik	Male	AK	4	2019	29 April	15 May	24 May	26
				5	2020	27 April	20 May	30 May	35
Ringed seal (<i>Pusa hispida</i>)	Pimniq	Male	AK	5	2019	2 May	15 May	24 May	23
				6	2020	26 April	4 May	17 May	22
Bearded seal (<i>Erignathus barbatus</i>)*	Noatak	Male	CA	5–6	2021	7 January	9 March	6 April	90

All seals were reproductively mature adults except one spotted seal (Kunik) during year 1 (2019) of the study. Peak (50%) molt is the date at which half of a seal’s new coat was present.

*The bearded seal exhibited a secondary shedding period after completing his molt in 2021; this occurred from 7 May–5 June, with no active coat regrowth.

minimal body moment and regular breathing intervals. When a seal completed a trial, whether during routine training or data collection, they received a large, predictable fish reward. No fish were given prior to trial completion, precluding metabolic changes associated with digestion.

Open-flow respirometry

RMR measurements were collected within enclosed chambers using open-flow respirometry as in Thometz et al. (2021). Briefly, ambient air was drawn through the chamber at a known rate between 150 and 200 l min⁻¹ using a Sable Systems mass flow controller (Sable Systems International, North Las Vegas, NV, USA). A subsample of excurrent air was dried through a column of Drierite (W A Hammond Drierite Co., Xenia, OH), scrubbed of carbon dioxide via a column of Sodasorb (Molecular Products Inc, Louisville, CO) and then dried again. Oxygen concentration was measured using a Sable Systems Field Metabolic System (AK: FC-1B, CA: FMS-1701-02) and recorded every second to a PC using Sable Systems *Expedata* software. Temperature and relative humidity were measured within each chamber to correct flow rates to standard temperature and pressure dry (STPD). Ambient environmental oxygen concentrations were determined prior to and following animal measurements to correct for any system drift. A given trial was considered valid if all behavioral criteria were met and a resting equilibrium value of oxygen consumption occurred for a period ≥ 4 min. For this reason, and because of the different air volumes within each chamber, session durations were typically shorter for in-water (11.6 \pm 2.9 min) trials compared with in-air (12.6 \pm 1.4 min) trials. Final rates of oxygen consumption for each seal were calculated using *Expedata* software, incorporating appropriate equations from Withers (1977). Absolute RMR values (ml O₂ min⁻¹) were scaled to mass-specific values (ml O₂ min⁻¹ kg⁻¹) to facilitate comparison between individuals and species that varied in body size (Table 1). Metabolic systems were calibrated before every session with ambient air and routinely checked for accuracy and leaks at each facility using standard methods (Davis et al., 1985; Fedak et al., 1981).

In-water setup

Seals voluntarily stationed under a custom-built acrylic dome affixed to a PVC frame that floated on the water's surface (Movie 1). In-water chambers were 101 cm long \times 90 cm wide \times 46 cm high, with a total air volume of approximately 150 l. A seal could choose to participate in a trial when a trainer entered the enclosure by moving under the dome and positioning calmly with its head above water for a sustained period of rest. Resting metabolic trials ranged from 5.9 to 18.2 continuous minutes in duration.

In-air setup

Seals voluntarily entered and then rested calmly within one of three custom-built metabolic chambers positioned on a haul out area when a trainer entered a seal's enclosure and provided access (Movie 2). The chambers in Alaska and California varied in dimensions and total volume based on the size of the seals at each facility (Table S1). These chambers were equipped with at least one door that sealed closed when the animal was inside. To minimize trial times, an initial ambient air flow rate of 40 l min⁻¹ was used to promote oxygen depletion within the chamber for up to 7.5 min or until the percentage of oxygen in the chamber had reached a level of 20.8%, at which point the flow rate was increased to 200 l min⁻¹ for the remainder of the session. Using this method, trial duration ranged from 8.2 to 16.6 min.

Molt status

Molt status was determined in the weeks leading up to, during, and following the annual molt using photographic records, molt characterization data sheets and daily scoring by husbandry staff. Metabolic data were later categorized as either molting or non-molting. The start of the molting period was defined as the first day of active hair loss and/or loose hair. The 50% molt date was defined as the date at which half of the seal's new coat was present; this was also considered peak molt. The end of the molt was defined as the last day of active hair loss and/or complete regrowth of the new coat (Table 1). Metabolic data were collected on each individual across the 2 month interval before the onset of molting, during the visible molt and for the 2 month period following the completion of molt. Data collected before and after the molting period were combined into the non-molt category.

Statistical analyses

Metabolic data were opportunistically collected throughout the annual study periods; however, only paired measurements (valid in-air and in-water trials taken within 48 h on the same individual) were included in statistical analyses (Table S1). Given apparent differences in bearded seal metabolism relative to the other seals and previous evidence that they differ in their metabolic response to molt (Thometz et al., 2021), we analyzed the spotted and ringed seal data separately from the bearded seal data. Metabolic data for spotted and ringed seals were combined and examined using a linear mixed-effects (LME) model. Mass-specific RMR data were assessed for normality prior to model building and log transformed to improve normality. We examined homogeneity of variance using Bartlett's test; neither molt status nor medium violated this assumption. Medium, molt status and the interaction between medium and molt status were included in the model as fixed effects. Seal (individual) was included as a random effect to account for repeated measures (Harrison et al., 2018). Fixed effects were considered significant at $P < 0.05$. Based on initial results, we could not reduce this model. Residuals of the model were plotted to confirm homoscedasticity and normality. Statistical analyses were performed using JMP16 statistical software (SAS Institute, Cary, NC). As there was only one bearded seal, we did not perform statistical analyses on these data, but summarize the results below for comparative purposes. Metabolic data for all species are presented as means \pm s.d.

RESULTS AND DISCUSSION

We found no evidence of elevated metabolic rates in Arctic seals that could be attributed to greater thermoregulatory costs imposed by the higher conductivity of water. Rather, paired measurements from individual ringed, spotted, and bearded seals evaluated across distinct physiological periods revealed comparable metabolic costs when resting in air and water (Fig. 1). It appears that a combination of thick insulating blubber and specialized circulatory adaptations facilitating efficient peripheral vasoconstriction (Favilla and Costa, 2020) allows these mammals to spend significant amounts of time in aquatic environments without notable metabolic repercussions. This finding supports the idea that marine mammals do not necessarily require greater energy budgets than terrestrial mammals to maintain aquatic or semi-aquatic lifestyles. Furthermore, this study contributes to the growing body of literature pertaining to the underlying physiological mechanisms and metabolic costs associated with molting in seals.

Molting was associated with a significant increase in metabolism for the spotted and ringed seals in both air and water (molt status: $F_{1,60} = 71.53$, $P < 0.0001$). This finding is consistent with previous

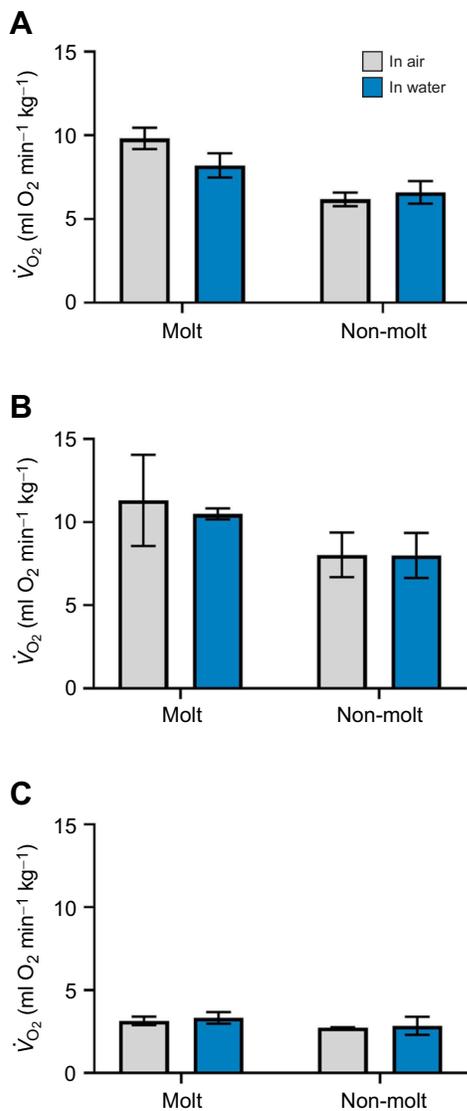


Fig. 1. In-air and in-water metabolic data for ice seals inside and outside the molting period. Paired in-air (gray bars) and in-water (blue bars) resting metabolic data for three spotted seals (A), one ringed seal (B) and one bearded seal (C). Individual data points and associated metadata are available in Table S1. Data are means \pm s.d.

reports of increased metabolism during molt in these polar species (Thometz et al., 2021), as well as in other phocid seals (Boily, 1996; Boily and Lavigne, 1997; Chabot and Stenson, 2002; Hedd et al., 1997; Renouf and Gales, 1994; Williams et al., 2011). Increased metabolic rates during the molting period have been variously attributed to the direct cost of tissue regeneration and/or the increased cost of heat loss to the environment associated with peripheral perfusion to promote that growth (Boily, 1995; Boyd et al., 1993; Feltz and Fay, 1966; Walcott et al., 2020). The latter is the assumed reason why seals spend increased amounts of time hauled out during the annual molt (Boily, 1995; Feltz and Fay, 1966). However, it is still unclear whether seals haul out to avoid increased heat loss from unavoidable/mandatory perfusion during the molt, or whether this behavior allows more opportunity for controlled perfusion and therefore a faster molt. The answer can be elucidated by examining how seals thermally respond to submersion in water – with its greater potential for heat loss – during this sensitive period.

We hypothesized that if seals were physiologically bound to continuous skin perfusion to facilitate pelage replacement, then they would experience severe energy losses in water compared with when hauled out during the molting period. We did not find evidence of this. Medium alone did not affect spotted or ringed seal metabolic rates (medium: $F_{1,59}=1.15$; $P=0.29$). Indeed, in-air and in-water measurements were remarkably similar within all individuals in this study (Table 2). This similarity in metabolism between media aligns with data reported for non-molting harbor seals (*Phoca vitulina*) measured within their thermal neutral zones, although lower critical temperatures for this species were lower in air than in water (Hart and Irving, 1959; Irving and Hart, 1957).

We did find an interaction between medium and molt status ($F_{1,59}=5.27$; $P=0.03$) for the spotted and ringed seals. While metabolism was higher during the molting period in both air and water, the difference in RMR between non-molting and molting periods was greatest when measurements were taken during haul out (Fig. 1A,B). Specifically, in-air RMR for spotted and ringed seals was 53% higher during molting (10.19 ± 0.91 ml O₂ min⁻¹ kg⁻¹) versus non-molting (6.64 ± 0.99 ml O₂ min⁻¹ kg⁻¹) conditions, compared with only 26% higher when measured in water (molt: 8.78 ± 1.29 ; non-molt: 6.95 ± 0.89 ml O₂ min⁻¹ kg⁻¹). In other words, the highest metabolic rates recorded for the seals in this study typically occurred when individuals were hauled out during molt and not, in fact, when they were in the water during this period (Table S1).

These data imply that spotted and ringed seals limit peripheral perfusion in water by maintaining fine-scale circulatory control regardless of molt status, as the thermal energetic consequences of skin perfusion in water would have been significant. Previous research has established that seals exhibit elevated surface temperatures during haul out reflecting increased skin perfusion (Erdsack et al., 2012; Mauck et al., 2003; Paterson et al., 2012; Walcott et al., 2020). We observed that spotted and ringed seals in this study maintained peripheral skin temperatures that were similar to that of seawater until well after haul out, when skin temperature increased by $>25^{\circ}\text{C}$ (our unpublished data; Fig. S1). Given such increased skin perfusion during haul out, it follows that the increased RMR in air during the molt reflects both the direct cost of tissue growth and the increased peripheral blood flow that facilitates it. We also propose that the observed difference in RMR values obtained in water between non-molting and molting periods largely reflects the direct cost of tissue regeneration. Thus the smaller difference in resting metabolism between the molting measurements obtained in water and during haul out seems to reflect the thermoregulatory costs of tissue perfusion, skin warming and associated heat loss to the environment. If this interpretation is correct, then the direct cost of tissue regeneration is a greater contributor to the overall cost of molting than the thermal consequences of tissue perfusion.

The bearded seal exhibited a different metabolic signature from the other two species. Based on visual examination of the RMR data (Fig. 1C) and treatment means (Table 2), neither molt status nor medium appeared to influence resting metabolism in this individual. This aligns with our previous work suggesting that bearded seals have a fairly stable RMR throughout the year (Thometz et al., 2021). The same study suggested that the much longer molt duration of bearded seals, relative to spotted and ringed seals (Table 1), serves to buffer the acute metabolic impacts of molt. We acknowledge that water temperatures for the bearded seal in this study were higher than those experienced by the other study animals and higher than

Table 2. Summary of resting metabolic data with five Arctic seals

Species	Seal ID	Mass (kg)	Non-molting RMR (ml O ₂ min ⁻¹ kg ⁻¹)		Molting RMR (ml O ₂ min ⁻¹ kg ⁻¹)	
			In air	In water	In air	In water
Spotted seal	Tunu	67–86	6.18±1.14 (5)	5.87±1.11 (5)	10.30±1.83 (2)	7.37±1.42 (2)
	Sura	53–62	5.78±0.50 (6)	6.70±0.70 (6)	9.09±1.40 (2)	8.55±0.14 (2)
	Kunik	54–69	6.58±0.66 (4)	7.22±0.57 (4)	10.07±1.85 (4)	8.70±1.06 (4)
Ringed seal	Pimniq	30–34	8.04±1.34 (6)	8.00±1.35 (6)	11.32±2.74 (4)	10.50±0.33 (4)
Bearded seal	Noatak	173–185	2.75±0.03 (2)	2.85±0.54 (2)	3.15±0.25 (4)*	3.33±0.35 (4)*

Data points are paired, thus each seal has the same number of points for each condition (non-molting vs. molting while hauled out or in water). Paired in-water and in-air measures were taken within 48 h. Values presented as means±s.d. (sample size, *n*). Individual data points with absolute values and associated metadata are available in Table S1.

*One set of paired points included with the molting data was obtained during the bearded seal's secondary shedding period.

temperatures typically experienced by free-ranging bearded seals; however, given the higher conductivity of water and its associated impacts we cannot attribute the lack of metabolic response during molt solely to differences in water temperature. Similar metabolic data from additional bearded seals across a range of temperatures and physiological states would help to clarify these issues.

Few studies have examined the role of haul-out behavior on metabolism during the molt in other pinnipeds. Two developmental studies lend additional context and support for the results described here. In Weddell seals (*Leptonychotes weddellii*; family Phocidae), the mass-specific RMR of pre-molt and molting pups was higher in water than when measured in air (Pearson et al., 2022). In contrast, RMR was comparable between in-air and in-water conditions for post-molt pups. Similarly, Donohue et al. (2000) found that the mass-specific RMR of pre-molt northern fur seal pups (*Callorhinus ursinus*; family Otariidae) in water was 2.8 times the in-air values. In post-molt pups, mass-specific metabolic rates were comparable in 20°C water and air. Thus, both Weddell seals and northern fur seals have the capacity to thermoregulate in water without the need for higher energy expenditures following their first molt. These studies provide insight into the effect of medium on metabolism in these species, but both are complicated by ontogenetic changes.

The Arctic seals included in this study maintained adequate control of peripheral circulation both during and outside the molting period to limit heat loss and associated energetic costs in water. This confirms that molting seals do not passively lose heat to their environment in an uncontrolled manner. Rather, since seasonal water temperatures for the focal species are well below the temperatures necessary for tissue regeneration (Feltz and Fay, 1966), seals probably haul out to implement a controlled increase in surface temperatures and peripheral blood flow to promote tissue regeneration (Fig. S1). If a lack of adequate haul out substrate or increased disturbance cause ice seals to increase time in water during the molting period, this will presumably limit the amount of time their skin is at the necessary temperature for tissue regeneration and lead to prolonged or unsuccessful molting. Such a disruption could have severe physiological and energetic consequences for individuals. Whether molting physiology, combined with reductions in haul out substrate (i.e. sea ice), has played a role in recent unusual mortality events declared for Alaskan ice seals (NOAA Fisheries, 2016, 2018) is something that should be investigated further.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: N.M.T., D.A.S.R., H.H.-S., C.R.; Methodology: N.M.T., D.A.S.R., C.R.; Validation: N.M.T., H.H.-S., M.M., M.P.; Formal analysis: N.M.T., D.A.S.R., H.H.-S., M.M., M.P.; Investigation: N.M.T., D.A.S.R., H.H.-S., M.M., M.P., C.R.; Resources: N.M.T., D.A.S.R., C.R.; Data curation: N.M.T., H.H.-S., M.M., M.P., C.R.; Writing - original draft: N.M.T., D.A.S.R.; Writing - review & editing: N.M.T., D.A.S.R., H.H.-S., M.M., M.P., C.R.; Visualization: N.M.T.; Supervision: N.M.T., C.R.; Project administration: C.R.; Funding acquisition: N.M.T., C.R.

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Data availability

All relevant data can be found within the article and its supplementary information.

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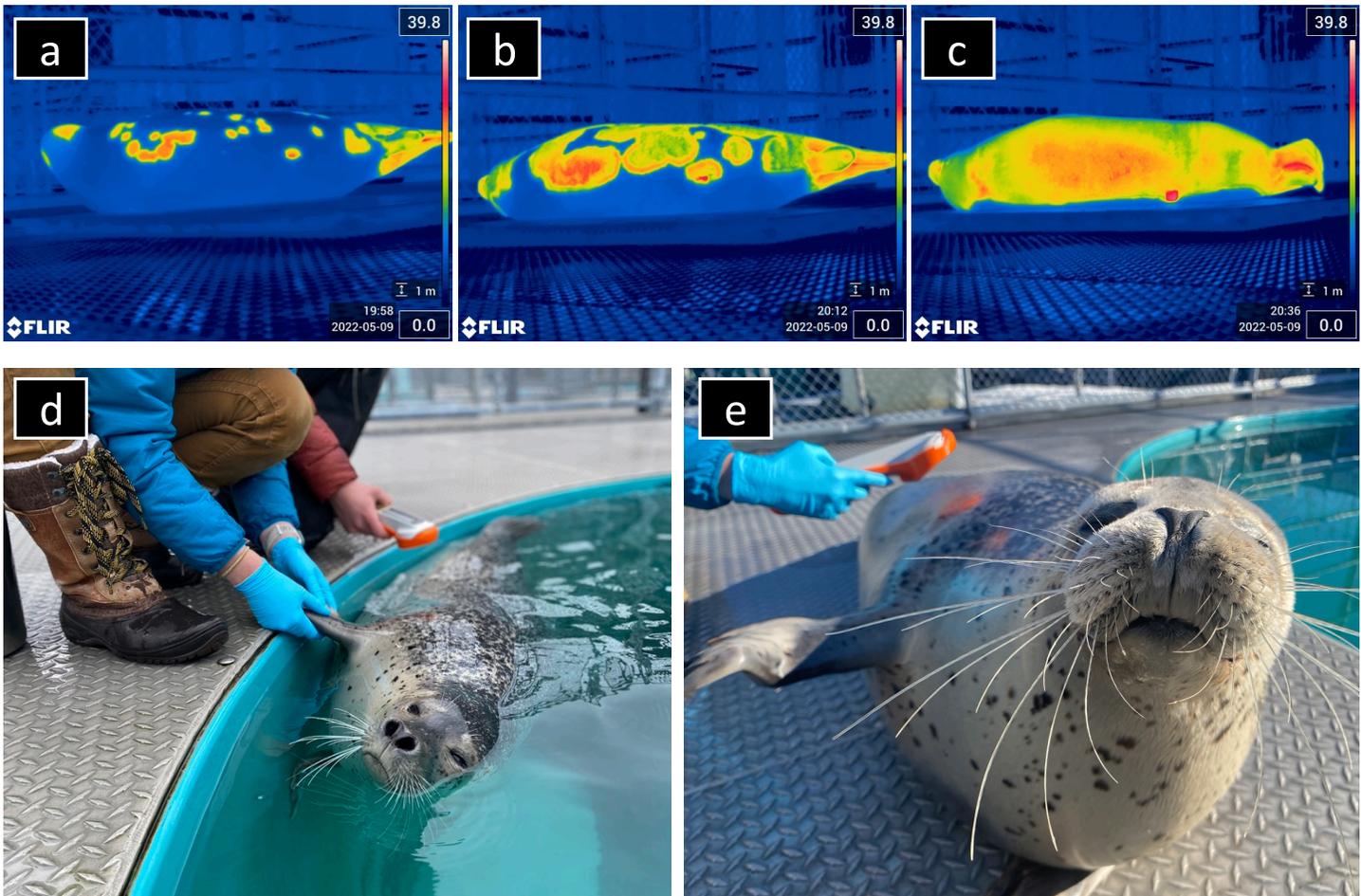


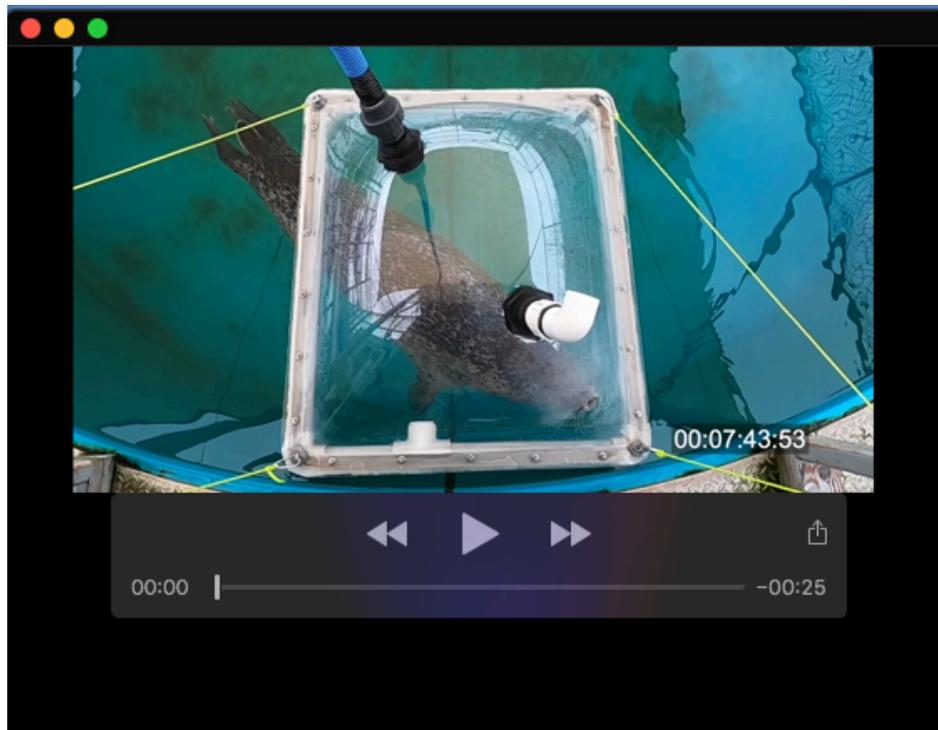
Fig. S1. Measures of surface temperatures in molting Arctic seals. Images shown here are from an 8 year-old (adult) female spotted seal at the Alaska SeaLife Center, although similar trends were observed from the three spotted seals and two ringed seals participating in the primary study (see Table 1). These patterns for ringed and spotted seals confirm surface temperature elevations $> 25\text{ }^{\circ}\text{C}$ when seals are resting out of water, including during molting periods when skin perfusion supports regeneration of hair and skin.

Serial infrared thermography (IRT) images (top row) were opportunistically obtained on 9 May 2022 with a FLIR T540 professional thermal camera (FLIR Systems Inc., Santa Barbara, CA) at a distance of 3 m. Images were obtained during early molt (scored as 5% new coat, -12 days from peak molt). The seal is resting on a composite wood platform on her left side, with her head to the left portion of the image and her back toward the camera. Images were taken using fixed camera settings and position following spontaneous haul out, with skin temperature patterns shown at (a) 16 min, (b) 30 min, and (c) 56 min following movement from the seawater pool (ambient water temperature $4.5\text{ }^{\circ}\text{C}$). The embedded temperature scale indicates recorded skin surface temperature variations. In general, seals showed surface temperatures on IRT images that varied from within a few degrees of the ambient water temperature to more than 25 degrees higher when skin temperature was greatest.

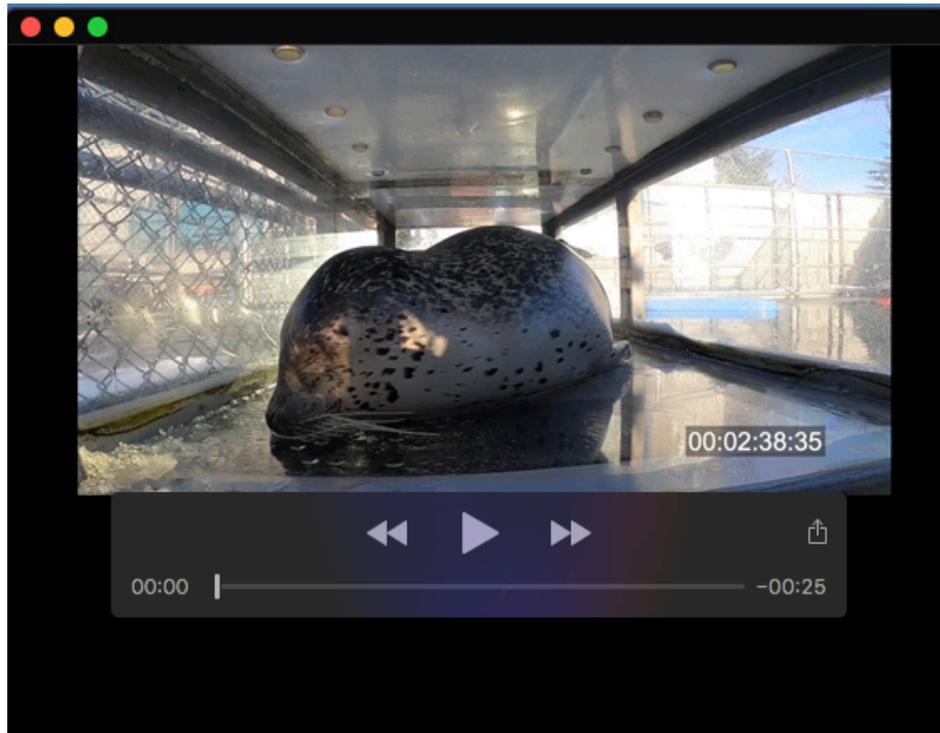
Subdermal skin temperatures (bottom row) were routinely measured from the same seal (d) in water and (e) following spontaneous haul out. Several IPTT-300 thermistor sensors (Bio Medic Data Systems, Seaford, DE) that could be read non-invasively using a Bluetooth reader (DAS-8027-BLU) had been placed into the dermis ($< 1\text{ cm}$ below skin surface) during routine veterinary examinations. Serial measurements from both ringed and spotted seals confirmed skin temperatures within a few degrees of ambient seawater when seals were in water or within a few minutes of haul out, with temperatures eventually increasing up to $35\text{ }^{\circ}\text{C}$. Absolute sub-dermal temperatures measured with thermistors aligned with regional temperatures derived from corresponding IRT images.

Table S1. Individual metabolic measurements and associated metadata. Table includes information about individuals at the time of data collection (species, location, sex, age, mass, daily energy intake), timing of data collection relative to molt status (date, molt status, days relative to peak (50%) molt, percent new coat at time of sampling), metabolic session condition (haul out, in water), environmental variables (air temperature, water temperature), measures of metabolism (absolute, mass-specific), and session variables (acclimation time prior to entering chamber, chamber size*, air flow rate, duration of data collection). Acclimation time refers to the amount of time an animal was in the medium (air or water) in which it was being measured prior to the initiation of a data collection session.

[Click here to download Table S1](#)



Movie 1. Example of voluntary (conditioned) behavior during metabolic data collection in water with adult female spotted seal *Sura*. Session date: 2021 05 22. Status: Post-absorptive, 65% molted. Condition: Resting in water. Trial duration: 11 min 57 s.



Movie 2. Example of voluntary (conditioned) behavior during metabolic data collection in air with adult female spotted seal *Sura*. This session was conducted 2021 03 21. Status: post-absorptive, not molting. Condition: Resting during haul out. Trial duration: 13 min 12 s.