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RESEARCH ARTICLE

Metabolic cost of thermoregulation decreases after the molt in developing Weddell seal pups

Linnea E. Pearson*, Emma L. Weitzner, Lars Tomanek and Heather E. M. Liwanag

ABSTRACT

Allocation of energy to thermoregulation greatly contributes to the metabolic cost of endothermy, especially in extreme ambient conditions. Weddell seal (*Leptonychotes weddellii*) pups born in Antarctica must survive both on ice and in water, two environments with very different thermal conductivities. This disparity likely requires pups to allocate additional energy toward thermoregulation rather than growth or development of swimming capabilities required for independent foraging. We measured longitudinal changes in resting metabolic rate (RMR) for Weddell seal pups (*n*=8) in air and water from one to seven weeks of age, using open-flow respirometry. Concurrently, we collected molt, morphometric and dive behavior data. Absolute metabolic rate (MR) in air followed the expected allometric relationship with mass. Absolute MR in water was not allometric with mass, despite a 3-fold increase in mass between one and seven weeks of age. Developmental stage (or molting stage), rather than calendar age, determined when pups were thermally capable of being in the water. We consistently observed post-molt pups had lower RMR in air and water (6.67±1.4 and 7.90±2.38 ml O_2 min^{-1} kg^{-1}, respectively) than pre-molt (air: 9.37±2.42 ml O_2 min^{-1} kg^{-1}, water: 13.40±3.46 ml O_2 min^{-1} kg^{-1}) and molting pups (air: 8.45±2.05 ml O_2 min^{-1} kg^{-1}, water: 10.4±1.63 ml O_2 min^{-1} kg^{-1}). RMR in air and water were equivalent only for post-molt pups. Despite the increased energy cost, molting pups spent three times longer in the water than other pups. These results support the idea of an energetic trade-off during early development; pups expend more energy for thermoregulation in water, yet gain experience needed for independence.

KEY WORDS: *Leptonychotes weddellii*, Resting metabolic rate, Metabolism, Thermal development, Phocid, Antarctica

INTRODUCTION

For homeotherms, maintenance of a relatively constant core body temperature is critical to all physiological functions (Somero et al., 2017). Because heat flows down a gradient, endotherms need to modulate heat flux to maintain a constant core body temperature (T_C). If heat loss exceeds heat production, T_C will decline; to compensate, endotherms will increase their metabolic rate (MR) (Scholander et al., 1950). Increasing MR is typically employed as an acute response to cold exposure (Scholander et al., 1950). Animals

Department of Biological Sciences, California Polytechnic State University, San Luis Obispo, CA 93401, USA.

*Author for correspondence (lepearso@calpoly.edu)

L.E.P., 0000-0002-2954-1359; E.L.W., 0000-0002-6871-3678; L.T., 0000-0002-9188-8038

may attempt to reduce heat loss over the long term by: (i) reducing the temperature gradient between themselves and the ambient environment, (ii) reducing surface area available for heat exchange, or (iii) increasing insulation.

Thermoregulation is critical for marine mammals because seawater is 25 times more conductive than air (Dejours, 1987). As pinnipeds (seals, sea lions, walruses) are endotherms that spend most of their life in water, this increased conductivity presents a thermal challenge that requires long-term strategies to overcome. At a relatively early developmental stage, young pinniped pups must successfully transition from a terrestrial to an aquatic environment. This is especially challenging for polar pinnipeds, as the harsh environment requires the allocation of additional energy toward thermoregulation rather than for growth or development. During early development it is important to reduce metabolic costs, such as those associated with thermoregulation, as initial foraging efforts may not be successful (Burns et al., 2005) and animals then rely on energy stores (i.e. blubber) to fuel metabolism.

The maintenance of thermoregulatory homeostasis may be especially costly for young phocids (true seals), as pups are typically born without the adaptations adults use to reduce thermoregulatory costs (Blix and Steen, 1979; Irving and Hart, 1957; Scholander et al., 1950). Instead of blubber, most phocids are born with a lanugo (newborn fur) coat (Elsner et al., 1977; Kvadsheim and Aarseth, 2002; Ling, 1974; Oftedal et al., 1991; Scholander et al., 1950). The insulative quality of fur depends on its ability to trap and warm a stagnant layer of air in the under-fur (Kvadsheim and Aarseth, 2002; Liwanag et al., 2012a; 2012b). For several species of phocid, pups first enter the water while they still have a lanugo coat; when the fur becomes wet, water replaces the trapped air and heat can be readily conducted away from the body (Davydov and Makarova, 1964; Elsner et al., 1977; Kvadsheim and Aarseth, 2002; Scholander et al., 1950). To compensate for increased heat loss, pups must increase their metabolic rate, activate another mechanism of heat production, or tolerate a decrease in body temperature to reduce the gradient between the body core and ambient environment. Additionally, pups need to develop insulation that is effective while submerged. Because phocid fur becomes saturated when submerged, pups must rely on blubber as their insulator in water (Kvadsheim and Aarseth, 2002; Liwanag et al., 2012a; 2012b; Pearson et al., 2019; Scholander et al., 1950; Sharma and Liwanag, 2017); thus, over the nursing period, pups rely on lipid-rich milk to rapidly deposit a blubber layer as they simultaneously molt their lanugo. The allocation of more energy toward insulation and fuel stores (i.e. blubber) during the dependence period may decrease metabolic costs in the water, and could sustain the pup through its aquatic transition, both by insulating it and by providing fuel for swimming and diving.

Molting pelage is itself an energetically expensive process and is associated with increased metabolic rate in adults of several phocid species (Boyd et al., 1993; Paterson et al., 2021; Thometz et al.,

Journal of Experimental Biology

1

2020). Molting requires energy to produce fur and to keep epidermal tissues metabolically active; animals must maintain skin temperatures well above ambient to properly perfuse hair follicles while growing new fur (Boily, 1995; Boyd et al., 1993; Ling, 1970). During this time, animals cannot/do not vasoconstrict blood flow to the skin, resulting in a steeper gradient between skin and ambient temperatures and increasing heat loss (Boily, 1995; Erdsack et al., 2012; Ling, 1970; Walcott et al., 2020). Furthermore, in pups, as lanugo is shed, the function of the primary insulator is compromised, increasing the conductivity of the pelt (Pearson et al., 2014a) and thus increasing the potential for heat loss if a sufficient blubber layer (or replacement insulation) is not fully developed (Pearson et al., 2019).

Weddell seals [*Leptonychotes weddellii* (Lesson 1826)] are the southernmost breeding mammal, and as such are born into an especially challenging thermal environment. While nursing, pups metabolize high-fat milk into a blubber layer; however, Weddell seals are initially born with a lanugo pelt and very little blubber (Pearson et al., 2014b; Tedman and Bryden, 1979). Among phocid seals in general, Weddell seals have one of the longest dependency periods and lowest rates of energy transfer from mother to pup (Oftedal et al., 1991). This may be enabled by the relative stability of fast ice, yet this prolonged dependency period may also be a function of high thermoregulatory costs. If pups must allocate a large proportion of energy toward thermoregulation, they will require a longer dependency period to acquire the resources necessary for morphological and physiological development prior to the transition to independence.

Weddell seal pups enter the water during the dependency period, as early as 2 days old (Elsner et al., 1977; Lindsey, 1937), and begin swimming and diving in addition to nursing and growing on ice (Burns and Testa, 1997; Weitzner et al., 2021). This appears to create an energetic trade-off between thermoregulation and diving during the critical dependency period: pups that wean at low weights (<80 kg) have a low probability of survival, but pups that spend more time in the water weigh less, possibly because of the high thermal costs of immersion (Hill, 1987). Pups can gain more weight by spending less time in the water, but this likely comes at a trade-off in terms of foraging skills and possibly development of diving capacity (Hill, 1987). Early water entry likely occurs before pups have developed the necessary insulation and physiology to deal with the greater conductivity of water, and this would be reflected by an increase in their resting metabolic rate (RMR) while in water compared with RMR in air, compensating for greater heat loss in water.

The aim of this study was to examine the transition from a terrestrial life to one in water by investigating capabilities of Weddell seal pups to deal with the increased thermoregulatory demands of submersion. We measured RMR in air and in water at four time points across dependency, beginning around pups' first water entry and concluding at or near the time of weaning: 1, 3, 5 and 7 weeks old. We determined whether pups increase metabolism to maintain euthermy or instead allow their body temperature to fluctuate in extreme cold. By comparing these values within individual pups and across ontogeny, we examined the effects of submergence on thermoregulatory energetic costs during development (Donohue et al., 2000). We hypothesized that young pups relying on lanugo for insulation would exhibit thermoregulatory costs in water (i.e. higher RMR in water than in air), that these energetic costs would be less pronounced as pups age and deposit a thicker blubber layer, and that variation in RMR due to thermoregulatory costs would be reflected in other metrics of heat

exchange. We predicted that pups would rely on lipid to fuel RMR in both air and water (measured by respiratory exchange ratio (RER) of ∼0.7) until weaning, when fuel use would shift toward a mix of lipid and protein (RER=0.8) to preserve lipid in the blubber for insulation, and that T_C would remain stable in both air and water across development, because pups would modulate RMR to maintain T_C, rather than lowering T_C to reduce RMR. Finally, we expected that whole body thermal conductance, a calculation of heat loss based on metabolic rate and ambient conditions, would be higher in younger pups with lanugo, especially when in water, as they may not have vasomotor control to reduce temperature gradients between the core and ambient environment.

MATERIALS AND METHODS
Animal capture and handling
Field work was conducted in McMurdo Sound, Erebus Bay, Antarctica (77°45′S, 166°30′E). Research procedures were conducted under National Marine Fisheries Service Permit No. 21006-01, California Polytechnic State University IACUC #1605 and #1904, and ACA permit #2018-013 M#1. During the austral springs (October–December) of 2017 and 2019, we handled 8 Weddell seal pups (6 males and 2 females; 4 pups per season) at 4 time points, representing 1, 3, 5 and 7 weeks of age. We targeted pups from multiparous females, as they have the highest likelihood of producing healthy pups (Chambert et al., 2014; Hadley et al., 2007a; Mannas, 2011). Life history data of target mothers were obtained from the long-term population monitoring study on this population (project B-009; J. Rotella and R. Garrott, Montana State University). We determined pup birth dates by direct observation, in collaboration with research group B-009, and conducted our measurements within 1–2 days of each target age time point.

Pups were separated from their mother (when present) using a herding board, captured using a custom-made mesh net (SLO Sail & Canvas, San Luis Obispo, CA, USA), then transported in a sled to our working location a safe distance from the mother. A veterinarian performed a health assessment before each procedure to ensure the pup was healthy. Mass (kg) was measured by weighing pups using a hanging electronic scale (±0.25 kg, Central Carolina Scale, Sanford, NC, USA) suspended from a tripod. After the full procedure, pups were transported back to the point of capture and reunited with the mother, unless the pup was older than 5 weeks and the mother was absent, or the pup had weaned. Mother–pup reunions were monitored for at least 30 min to ensure they remained bonded, and lone pups were monitored for 30 min to ensure full recovery.

The molt status of each pup was determined at each handling by visual inspection of the pelage and the pup was assigned to one of three groups: pre-molt (full lanugo), molting (shedding lanugo) or post-molt (no lanugo present). Morphometric measurements including girth, curvilinear length, height and width were taken at 8 sites along the body according to Shero et al. (2014). Subcutaneous blubber thickness was measured using ultrasound (Sonosite 180+, FUJIFILM Sonosite Inc., Bothell, WA, USA) at six dorsal and lateral sites (Shero et al., 2014). Body composition was estimated using a series of elliptical cones, and percentage blubber was calculated from estimates of blubber and lean tissue volumes (Shero et al., 2014). At the 1-week time point, each pup was equipped with a time–depth recorder (TDR) to record dive behavior. Dive data [depth (m)] were recorded every 4 s at a resolution of 0.5 m while the TDR was wet, and data were averaged for ±2 days around the date of the metabolic rate trial for each pup (for the 1-week time point, only +2 days data were available). Dive data collection and processing are further described in Weitzner et al. (2021).

Metabolic rate measurements

We measured the RMR of pups using flow-through indirect calorimetry at each age time point and report both absolute metabolic rate (MR; ml O_2 min^{-1}) and mass-specific metabolic rate (msMR; ml O_2 min^{-1} kg^{-1}). Measurements were completed on pups in two treatments: in air (designated MR$_A$ and msMR$_A$) and in water (designated MR$_W$ and msMR$_W$). We used a metabolic chamber custom-fabricated from a Pelican container (BL8024-3009, Pelican Products, Inc., Torrance, CA, USA) with interior dimensions (L×W×D) of 204.3×62.1×99.7 cm and exterior dimensions of 214.5×72.2×111.3 cm. The chamber was modified with hose fittings on either end of the lid and six Plexiglas viewing windows around the lid to allow for behavioral monitoring. The chamber was airtight when closed, with the exception of the installed ports for air flow. We placed a custom-fitted plastic platform on the bottom of the chamber to provide support for the animals. For 1-week-old pups only, we placed a plastic divider inside the chamber, approximately 150 cm from one end, to limit their movements.

Resting metabolic rates were measured only in air for 1-week-old pups to reduce handling time for dependent pups at such a young age. For pups at 3, 5 and 7 weeks, we measured RMR first in air and then in water for each pup; logistical constraints prevented us from being able to randomize the order of trials. An experimental session consisted of a 30–40 min data acquisition period after 5–10 min of acclimatization in the metabolic chamber under each treatment (air or water), with each animal tested once per treatment at each time point. For pups 3 weeks and older, the animal was removed from the metabolic chamber after the trial in air and allowed to rest nearby while we pumped ambient seawater from a hole through the sea ice into the chamber using a gear drive pump (Magnatex, Houston, TX, USA). We filled the chamber with water to a level that would submerge the animal to its torso but allow its head to remain above water and discourage swimming. In-chamber ambient air (T_a; °C) and water temperatures (T_w; °C) were recorded at the beginning and end of each trial. Core body temperature (T_C; °C) of the animal was recorded before and after each trial using a flexible rectal probe (RET-12, Physitemp Instruments Inc, Clifton, NJ, USA) inserted 15 cm into the rectum. Animal behavior was continuously monitored and recorded throughout each trial. Pups were kept awake by gently tapping on the chamber if they attempted to sleep during the trial. Whereas traditional standard conditions for metabolic measurement (described by Kleiber, 1975) call for animals to be in a post-absorptive state, we could not adhere to this condition because of concerns about animal welfare. No attempts were made to fast pups before trials. In 2019, absorptive state was determined by a visual inspection of lipemia in the blood serum (collected as part of larger study objectives; no blood was collected in 2017). We compared RMR between lipemic ($n=11$) and non-lipemic ($n=5$) (post-absorptive) pups to test the suitability of combining data. Pups met the following Kleiber criteria: quiescent, awake, nonpregnant and nonlactating.

For all trials, ambient air was drawn through the chamber at 500 l min^{-1}, with flow rates maintained and monitored continuously by a mass flow controller (Flowkit 500, Sable Systems, Henderson, NV, USA). Air was sampled from the exhaust port of the chamber at 100 ml min^{-1} and measured for water vapor, O_2 content, and CO_2 content (Field Metabolic System, Sable Systems, Henderson, NV, USA). The percentage of O_2 in the expired air was monitored continuously and recorded once per second with a field laptop (Panasonic Toughbook CF-31) using ExpeData software (Expedata PRO version 1.9.13; Sable Systems, Henderson NV, USA).

Following the equations of Lighton (2018), we corrected measured gas values to standard temperature and pressure and calculated the rate of O_2 consumption ($\dot{V}_{O_2}$; ml O_2 min^{-1}) and CO_2 production ($\dot{V}_{CO_2}$; ml CO_2 min^{-1}) for a 5–10 min period corresponding with continuous quiescent behavior. These data were used to calculate the respiratory exchange ratio (RER=$\dot{V}_{CO_2}/\dot{V}_{O_2}$) for each pup in each treatment at each age time point. Mass-specific metabolic rates (air: msMR$_A$; water: msMR$_W$) were calculated by dividing MR by mass for each treatment and age. We calibrated the system at the beginning and end of each field season with N_2 gas according to Fedak et al. (1981) and a dry span gas (2.0% CO_2) and daily with ambient air scrubbed of water (Drierite; Hammond Drierite, Xenia, OH, USA) and of carbon dioxide (Ascarite; Acros Organics, NJ, USA).

Thermal conductance

Whole body thermal conductance C (ml O_2 kg^{-1} h^{-1}°C^{-1}) for each pup at each age and treatment was calculated according to McNab (1980):

$$C = Q/(T_C - T_E),$$

where Q is heat loss or production (msMR in ml O_2 kg^{-1} h^{-1}), T_C is core body temperature (°C), and T_E is environmental temperature (°C) inside the metabolic chamber: T_a in air trials and T_w in water trials (Donohue et al., 2000). T_C and T_E were measured before and after each trial, and the mean of each was used for calculations.

Analyses

Prior to analysis, data were tested for suitability for linear modeling. We examined response variables for normality using *QQ* Plots and Shapiro–Wilk normality test, and examined RMR data for outliers using the box-plot method [function identify_outliers in R (https://www.r-project.org/)]. There were no significant differences in RMR between pups that were lipemic and those that were not lipemic, so data were combined for analyses. Data are reported as mean±1 s.d., and statistical significance was considered at α=0.05.

Metabolic rate comparison

We used simple linear regression to investigate the relationship between log-transformed mass (kg) and log-transformed MR (ml O_2 min^{-1}). We found that MR$_W$ did not follow an allometric relationship with mass (Fig. 1), so both MR and msMR were analyzed for each treatment rather than focusing solely on msMR.

MR and msMR at each age time point were compared between air and water, and changes across ages were compared within a treatment (air or water) using mixed measures ANOVA with Bonferroni-corrected multiple pairwise *post hoc* comparisons using the rstatix package in R (https://CRAN.R-project.org/package=rstatix). Within a treatment (air or water), we tested for differences in MR or msMR by molt status using mixed measures ANOVA with individual ID as the between-subject factor and molt status as the within-subject factor, with Bonferroni-corrected *t*-test *post hoc* comparisons.

Metrics of heat exchange

Respiratory exchange ratios (RERs) were compared between air and water trials at each age time point using a two-way mixed measures ANOVA with age (in weeks) as the between-subject factor and treatment as the within-subject factor, and *post hoc* analyses were done using *t*-tests with Bonferroni corrections. To test if weaning affected RER within a treatment, we compared RER between
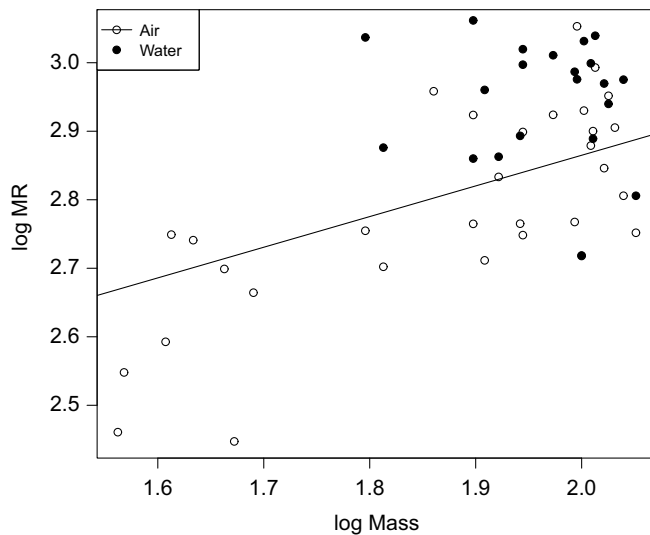
Fig. 1. Resting metabolic rate in air and in water as a function of body mass for 1- to 7-week-old Weddell seal pups (n=8). Data represent repeated measures across the 4 age time points in air (open circles) and in water (solid circles). There was a significant relationship between mass (kg) and metabolic rate (MR; ml O$_2$ min^{-1}) in air (solid line; $F_{1,29}$=34.44, P<0.001, R^2=0.5271) but no relationship between mass and metabolic rate in water (R^2=−0.04).

independent (weaned) and dependent pups within a treatment using t-tests with Bonferroni corrections.

Rectal temperature was used as a proxy for T_C (°C). Pre-trial T_C were compared between treatments at each age time point, and between treatments by molt status using separate mixed measures ANOVA with individual ID as the between-subject factor and treatment as the within-subject factor. *Post hoc* analyses were done with t-tests with Bonferroni corrections. Change in body temperature (ΔT_C: post-trial T_C–pre-trial T_C) was compared between treatments (air versus water) and among ages using separate two-way mixed measures ANOVA with individual ID as the between-subject factor and treatment as the within-subject factor, and *post hoc* analyses were done using t-tests with Bonferroni corrections. Differences in ΔT_C within each treatment among molt statuses and between independent and dependent pups were compared using t-tests with Bonferroni corrections.

Whole body thermal conductance was compared between treatments and among age time points using separate two-way mixed measures ANOVA with age (in weeks) as the between-subject factor and treatment as the within-subject factor. Conductance was also compared within each treatment by molt status using a two-way mixed measures ANOVA with individual ID as the between-subject factor and molt status as the within-subject factor, and *post hoc* analyses were done using t-tests with Bonferroni corrections.

Effects of body composition and dive parameters

We used two-way mixed measures ANOVA to compare a series of dive behavior metrics (dependent variables: amount of time spent in the water (s), total number of dives (n dives), maximum dive depth (m), mean dive depth (m), mass (kg) and body composition (% blubber) by molt status (pre-molt, molting, post-molt; independent variable). Mass and body composition, as metrics of pup growth, were also compared by age time point. *Post hoc* comparisons were done between groups using t-tests with Bonferroni corrections.

During development, there are many confounding and underlying factors that contribute to thermoregulation and metabolic rates. To evaluate the relationships and sources of variation among RMR amongst physiological predictors typically associated with thermoregulation (mass, % blubber, blubber depth, etc.), we ran a series of linear mixed effects models (LMEs) with restricted maximum likelihood (REML) estimation using the glmmTMB package in R (https://CRAN.R-project.org/package=glmmTMB). Additionally, to determine if individual differences in dive development correlated with RMR development, we ran LME using metrics of dive behavior to parameterize the model. MR and msMR were evaluated as response variables and air and water treatments were analyzed in separate LMEs. Physiological predictor variables included: % blubber, molt status (pre-molt, molting, post-molt), an interaction term between % blubber and molt status to account for collinearity, and ΔT_C as fixed effects, and individual ID as a random effect to account for repeated measures. Models with dive parameters included mean dive depth (m), mean dive duration (s) and number of dives (n dives) as fixed effects, and individual ID as a random effect. Mass was included as a predictor variable in all MR models to account for any underlying relationship between MR and mass. Models were ranked using Akaike information criteria (AICc), log likelihoods (logLik) and R^2. Residual plots were examined to assess model fit. The variance explained by the random effect was assessed based on the difference in the marginal (fixed effects only) and conditional (all model variables) R^2 (rsquared, glmm function).

RESULTS

Although analysis revealed several statistical outliers in our metabolic rate dataset, these outliers were not the result of a behavioral abnormality (e.g. sleeping, overly active), nor was one individual repeatedly an outlier for any metric. We chose to retain the outliers in our dataset, as we found no biological reason to censor them. We ran all analyses with and without outliers to determine if they had undue influence on our statistical results given our small sample size and determined no statistically significant patterns were driven solely by inclusion of outlier values. Ambient temperature conditions in the metabolic chamber are reported in Table 1.

Table 1. Ambient conditions inside the metabolic chamber during respirometry trials with 1- to 7-week-old Weddell seal pups

Age (weeks)	Air		Water			
	T_a pre-trial (°C)	T_a post-trial (°C)	T_a pre-trial (°C)	T_a post-trial (°C)	T_w pre-trial (°C)	T_w post-trial (°C)
1	1.35±1.63	1.74±2.42	n.a.	n.a.	n.a.	n.a.
3	5.57±3.78	5.12±3.47	4.69±3.12	4.19±1.79	−1.59±0.18	−0.81±0.90
5	10.35±3.81	10.65±4.97	9.96±4.39	10.01±3.90	−1.55±0.17	0.45±0.99
7	8.40±3.46	8.36±3.15	8.02±3.58	7.91±4.19	−1.47±0.14	0.14±0.91

Air (T_a) and water (T_w) temperature (°C) (means±s.d.) were measured inside the metabolic chamber at the beginning (pre-trial) and after the completion (post-trial) of the metabolic trial at each age time point.

Metabolic rate

The relationship between MR_W and mass was non-allometric and was not significant ($R^2=-0.04$; Fig. 1). The relationship between MR_A and mass, which also included measurements from 1-week-old pups, was significant ($F_{1,29}=34.44$, $P<0.001$, $R^2=0.5271$; Fig. 1) and followed the equation $\log(MR_A)=1.53+0.67[\log(\text{mass})]$; this relationship was driven largely by MR of the 1-week-old pups. On average, MR_A doubled between 1 and 5 weeks of age (423 ± 112 ml O_2 min^{-1} to 837 ± 157 ml O_2 min^{-1}) and declined at 7 weeks (678 ± 148 ml O_2 min^{-1}) (Fig. 2A). There was a significant effect of age on MR_A ($F_{1,29}=12.614$, $P=0.001$), such that MR_A at 1 week was significantly lower than MR_A at 3, 5 and 7 weeks ($P<0.05$), but MR_A values at 3, 5 and 7 weeks were not different from each other. MR_W was variable (3 weeks: 908 ± 178 ml O_2 min^{-1}; 7 weeks: 832 ± 240 ml O_2 min^{-1}) and was not significantly different across ages ($F_{1,20}=0.602$, $P=0.447$) (Fig. 2A). When we compared MR between air and water within an age time point, MR_W was significantly greater than MR_A at 3 weeks ($P=0.00869$) and 5 weeks ($P=0.0127$). At 7 weeks, there was no significant difference between MR_A and MR_W (Fig. 2A).

MR_A varied significantly with molt status ($F_{2,28}=14.278$, $P<0.001$; Fig. 2B) and *post hoc* analysis showed MR_A was significantly lower for pre-molt pups (456 ± 110 ml O_2 min^{-1}) compared with molting (772 ± 170 ml O_2 min^{-1}; $P<0.001$) and post-molt (694 ± 156 ml O_2 min^{-1}; $P=0.0116$) pups. MR_A was not significantly different between molting and post-molt pups (Fig. 2B). There was no significant effect of molt status on MR_W (pre-molt: 945 ± 174 ml O_2 min^{-1}; molting: 966 ± 127 ml O_2 min^{-1}; post-molt: 809 ± 254 ml O_2 min^{-1}; Fig. 2B). When we compared MR between air and water within a molt status, MR_W was significantly greater than MR_A for both pre-molt and molting pups ($P<0.001$ and $P=0.003$, respectively), but not for post-molt pups (Fig. 2B).

Mass-specific metabolic rate

As expected, given the co-linearity between mass and age, $msMR_A$ declined from 9.98 ± 2.50 ml O_2 min^{-1} kg^{-1} in 1-week-old pups to 6.65 ± 1.31 ml O_2 min^{-1} kg^{-1} in 7-week-olds, with a high degree of individual variability (Fig. 3A). There was a significant effect of age on $msMR_A$ ($F_{1,29}=9.884$, $P=0.004$), such that $msMR_A$ was significantly lower at 7 weeks than at 1 week ($P=0.0195$). There were no significant differences in $msMR_A$ among the other ages. $msMR_W$ subjectively appeared to decline from 3 weeks (12.0 ± 3.06 ml O_2 min^{-1} kg^{-1}) through 7 weeks (8.18 ± 2.29 ml O_2 min^{-1} kg^{-1}), but there were no statistically significant differences across ages (Fig. 3A). When compared between treatments, $msMR_W$ was significantly greater than $msMR_A$ at 3 weeks ($P=0.023$) and 5 weeks ($P=0.0353$), but not at 7 weeks of age.

$msMR_A$ generally decreased as molting progressed, though there were no statistically significant differences among molt groups (pre-molt: 9.37 ± 2.42 ml O_2 min^{-1} kg^{-1}; molting: 8.45 ± 2.05 ml O_2 min^{-1} kg^{-1}; post-molt: 6.76 ± 1.40 ml O_2 min^{-1} kg^{-1}; Fig. 3B). $msMR_W$ decreased significantly as molting progressed ($F_{1,20}=14.769$, $P=0.001$), such that $msMR_W$ was significantly lower in post-molt pups (7.90 ± 2.38 ml O_2 min^{-1} kg^{-1}; $P=0.004$) compared with pre-molt pups (13.40 ± 3.46 ml O_2 min^{-1} kg^{-1}). For molting pups, $msMR_W$ (10.40 ± 1.63 ml O_2 min^{-1} kg^{-1}) was not significantly different from pre-molt or post-molt pups (Fig. 3B). As with the pattern observed in MR, when we compared $msMR_A$ and $msMR_W$ across molt status, $msMR_W$ was significantly greater than $msMR_A$ in pre-molt pups ($P=0.0351$) and molting pups ($P=0.0137$) but there was no significant difference between $msMR_W$ and $msMR_A$ for post-molt pups (Fig. 3B).

Metrics of heat exchange

RER ranged from 0.796 ± 0.06 to 1.040 ± 0.09 in air and 0.774 ± 0.08 to 0.844 ± 0.16 in water (Table 2); there was no significant difference
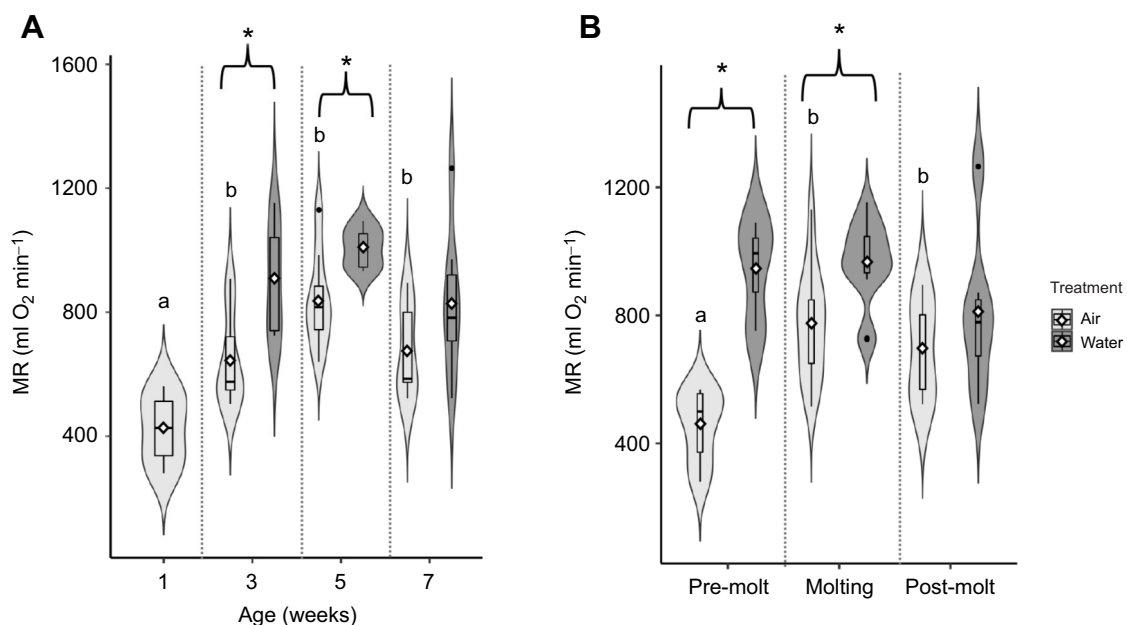

Fig. 2. Resting metabolic rate for Weddell seal pups (*n*=8) in air and water by pup age and molt status. MR as a function of (A) pup age (weeks) and (B) molt status in air (light grey) and in water (dark grey). Mean (white diamond), median (hash), outliers (solid circle), and quartiles (whiskers) of data are shown. Different letters indicate significant differences (*P*<0.05) among measurements in air; groups (age or molt status) with the same letter indicate no significant difference among groups (*P*>0.05). There were no significant differences among measurements in water. *Significant difference (*P*<0.05) between air and water within a given group (age or molt status). Dashed lines between groups are added for visual clarity.
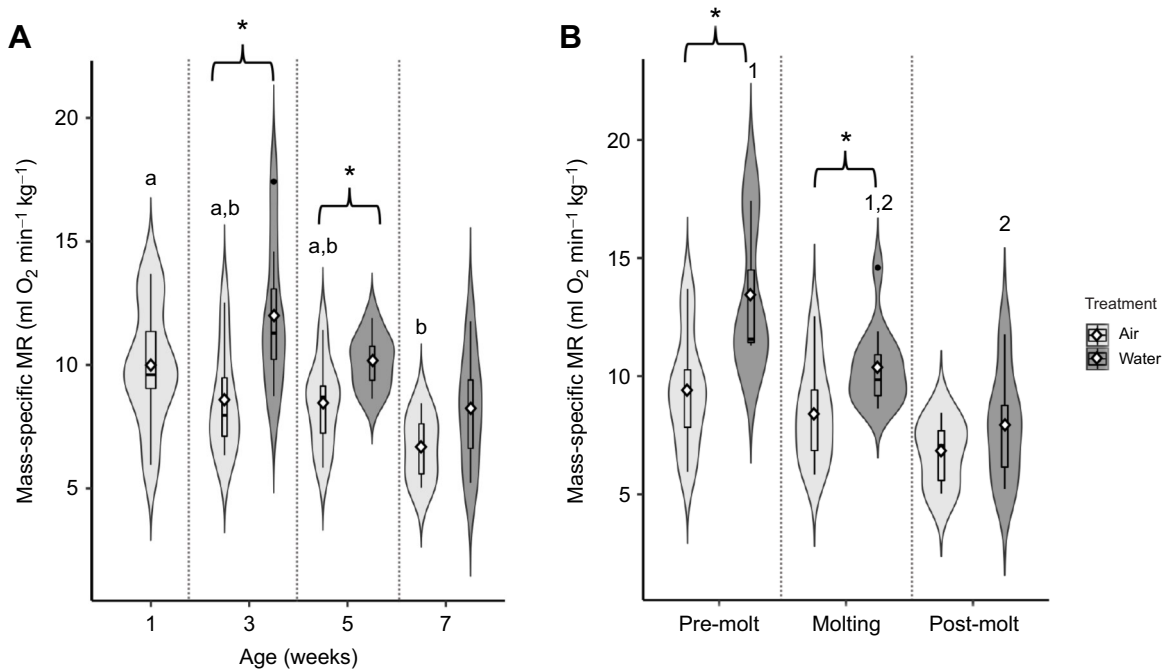
Fig. 3. Mass-specific metabolic rate for Weddell seal pups (n=8) in air and water by pup age and molt status. msMR as a function of (A) pup age (weeks) and (B) molt status in air (light grey) and water (dark grey). Mean (white diamond), median (hash), outliers (solid circle), and quartiles (whiskers) of data are shown. Different letters indicate significant differences ($P<0.05$) for measurements in air; groups (age or molt status) with the same letter indicate no significant difference among measurements in air ($P>0.05$). Different numbers indicate significant differences for measurements in water; groups (age or molt status) with the same number indicate no significant difference among measurements in water ($P>0.05$). *Significant difference ($P<0.05$) between air and water within a given group (age or molt status). Dashed lines between groups are added for clarity.

between treatments or among ages. Within a treatment, there was no significant difference among molt groups. Between treatments, RER was significantly higher in air than in water for molting pups ($P=0.0437$; Table 2). There was no significant difference in RER between air or water for dependent and independent pups, though in air, independent pups tended to have a lower RER on average. Further, there were no significant differences in RER between lipemic and non-lipemic animals.

Core body temperature (T_C) was lower at the end of a trial than at the beginning of a trial across treatments and ages (a negative ΔT_C), but the decline was typically less than 1°C (Table 2). At the 3- and 5-week age time points, pre-trial T_C was significantly lower at the start of the water trial than at the start of the air trial (3 w: $P=0.0474$; 5 w: $P=0.003$). This was driven by the difference in pre-trial T_C between molting and non-molting animals, as pre-trial T_C was significantly lower at the start of water trials than air trials for molting pups

Table 2. Changes in respiratory exchange ratio (RER), core body temperature (T_C; °C), and thermal conductance by treatment (air or water) and group (age, weaning status and molt status)

Treatment	Group (n)	RER	Pre-trial T_C (°C)	$\triangle T_C$ (°C)	Thermal conductance (ml O_2 kg^{-1} h^{-1} $°C^{-1}$)
Air	1 week (8)	0.823±0.27	37.2±0.4	−0.014±0.54	17.0±4.3
	3 week (8)	1.040±0.09	37.0±0.5[a]	−0.488±0.86	16.7±5.1
	5 week (8)	0.877±0.13	36.9±0.3[a]	−0.600±0.52	19.6±6.2
	7 week (7)	0.796±0.06	36.4±0.6	−0.100±0.27[a]	14.3±2.7
	Dependent (25)	0.925±0.17	–	−0.348±0.69	17.7±5.1
	Independent (6)	0.788±0.06	–	−0.233±0.33	13.7±2.7
	Pre-molt (11)	0.911±0.23	37.1±0.6	−0.10±0.6	16.5±4.24
	Molting (14)	0.929±0.14[a]	37.0±0.3[a]	−0.58±0.6	18.3±5.91
	Post-molt (6)	0.797±0.06	36.4±0.6	−0.06±0.3[a]	14.7±2.69
Water	1 week (8)	–	–	–	–
	3 week (7)	0.844±0.16	36.4±0.6	−0.771±0.65	19.5±6.2
	5 week (8)	0.774±0.08	36.3±0.4	−0.500±0.84	16.4±1.8
	7 week (7)	0.802±0.10	36.4±0.6	−0.617±0.32	13.4±3.7
	Dependent (25)	0.820±0.13	–	−0.600±0.74	17.4±4.1
	Independent (6)	0.767±0.07	–	−0.683±0.38	14.0±4.2
	Pre-molt (3)	0.731±0.01	36.4±0.2	−0.57±0.7	21.8±5.49[b]
	Molting (13)	0.820±0.13	36.4±0.5	−0.62±0.8	16.8±2.69
	Post-molt (6)	0.811±0.10	36.4±0.7	−0.66±0.3	13.0±3.89

Values are means±s.d. Letters in superscript indicate significant differences ($P<0.05$): [a]Significantly different from water treatment; [b]Significantly different from post-molt. 'n' values for age groups indicate number of individuals when grouped by age; for all other groups, 'n' values represent the number of repeated measure replicates.

($P<0.001$), but not for non-molting pups. ΔT_C varied significantly by treatment ($F_{1,46}=5.569$, $P=0.023$), but not by age (Table 2). *Post hoc* analysis showed at the 7-week time point, T_C decreased significantly more during water trials (-0.617 ± 0.32°C) than air trials (-0.100 ± 0.27°C; $P=0.009$). There was no significant difference in ΔT_C between air and water treatments for the 3- and 5-week time points (Table 2). ΔT_C decreased significantly more in air trials compared to water trials for post-molt pups ($P=0.014$), but not for pre-molt or molting pups. There were no significant differences in ΔT_C between dependent and independent pups.

Total body thermal conductance varied by age in air (range: 14.3 ± 2.7–19.6 ± 6.2 ml O$_2$ kg^{-1} h^{-1}), and in general declined with age in water (19.5 ± 6.2 ml O$_2$ kg^{-1} h^{-1} at 3 weeks to 13.4 ± 3.7 ml O$_2$ kg^{-1} h^{-1} at 7 weeks), though there were no significant differences in conductance among ages in air or water, or between air and water at any age (Table 2). There was no significant difference in conductance between dependent and independent pups within or between each treatment (Table 2). When conductance was compared among molt status categories, there were no significant differences in air trials. In water, pre-molt pups had significantly greater thermal conductance

(21.8 ± 5.49 ml O$_2$ kg^{-1} h^{-1}) than post-molt pups (13.0 ± 3.89 ml O$_2$ kg^{-1} h^{-1}; $P=0.005$; Table 2). There was no significant difference in conductance between molting pups and pre-molt or post-molt pups. Conductance in water was not correlated with ambient water temperature or the change in water temperature pre-trial to post-trial. Further, there was no correlation between conductance and water temperature or molt status.

Effects of dive parameters, mass, and body composition

Time spent in the water ($F_{1,29}=1.557$, $P=0.05$) was the only dive parameter that varied significantly among molt groups. Molting pups spent significantly more time in the water than either pre-molt ($P<0.001$) or post-molt pups ($P<0.001$). There was no significant difference in the amount of time spent in the water between pre-molt and post-molt pups (Fig. 4A). While not significant at the 95% level, in general, molting pups made more dives than pre-molt pups (Fig. 4B); however, pre-molt and molting pups did not dive as deep as post-molt pups (Fig. 4C,D).

Mass increased significantly with age ($F_{3,27}=111.892$, $P<0.001$; Fig. 5A), and was significantly different ($P<0.001$) among all age time points except between 5- and 7-week-old pups. Mass also varied by molt status ($F_{2,28}=45.348$, $P<0.05$; Fig. 5B), such that
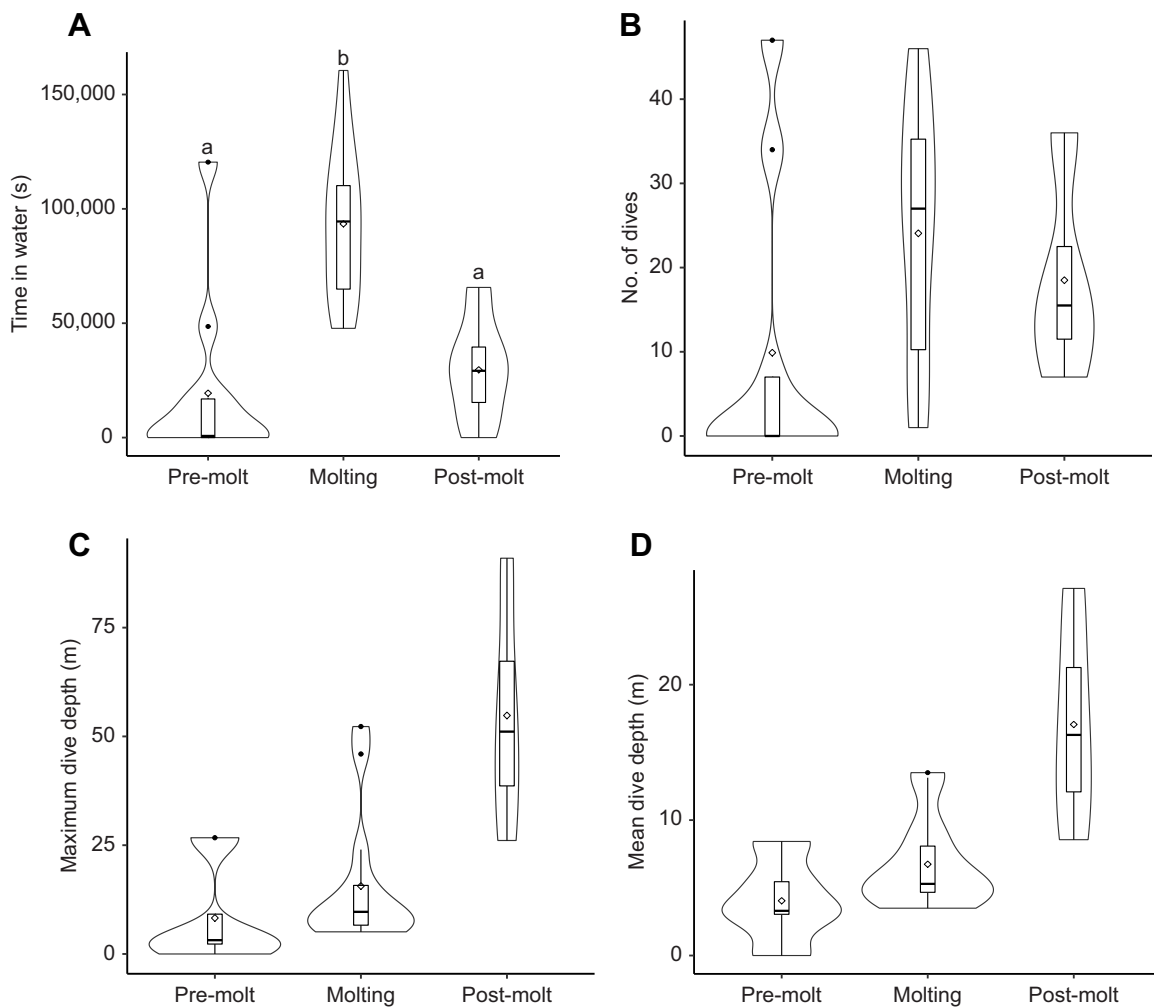

Fig. 4. Dive parameters of Weddell seal pups (*n*=8) compared by molt status. (A) Time spent in the water (s). (B) Number of dives. (C) Maximum dive depth (m). (D) Mean dive depth. Mean (white diamond), median (hash), outliers (solid circle) and quartiles (whiskers) of data are shown. Dive data are an average of activity±2 days from a handling event. Different letters indicate significant differences among molt status groups (*P*<0.05). Groups with the same letter indicate no significant difference between groups (*P*>0.05).
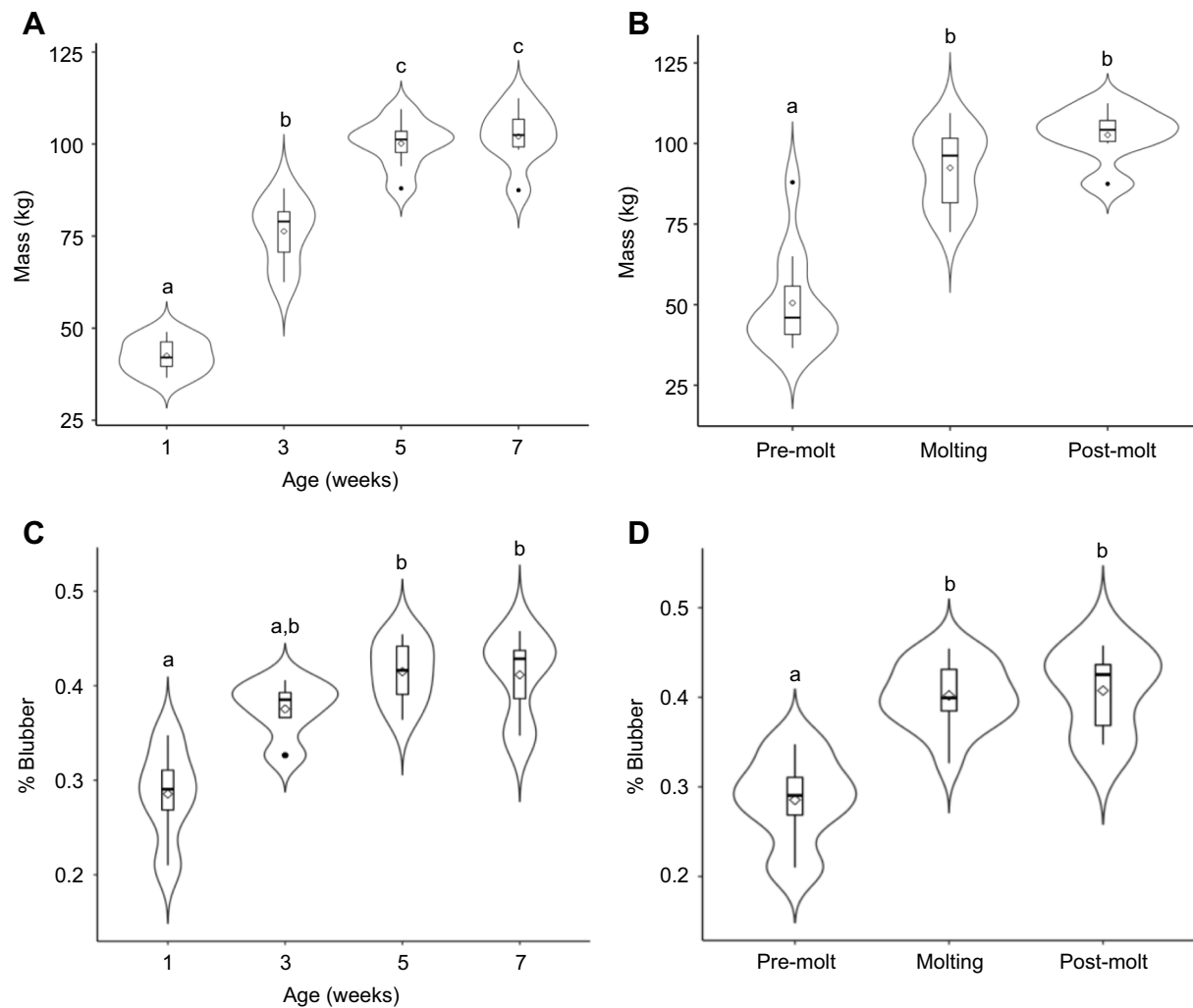
Fig. 5. Mass and body composition of Weddell seal pups (*n*=8) compared by age and molt status. Mass (A,B) and body composition (% blubber; C,D) as a function of (A,C) age (weeks) and (B,D) molt status. Mean (white diamond), median (hash), outliers (solid circle) and quartiles (whiskers) of data are shown. Different letters indicate significant differences among age or molt status groups (*P*<0.05). Groups with the same letter indicate no significant difference between groups (*P*>0.05).

pre-molt pups had significantly less mass than molting (*P*<0.001) or post-molt pups (*P*<0.001), but there was no significant difference in mass between molting or post-molt pups (Fig. 5B).

Body composition significantly varied by age ($F_{3,21}$=12.839, *P*<0.001; Fig. 5C). One-week-old pups had a significantly smaller proportion of blubber than pups at 5 weeks (*P*=0.014) and 7 weeks (*P*=0.013) of age (Fig. 5C); no other ages were significantly different from each other. Body composition also varied significantly with molt status ($F_{2,22}$=15.903, *P*<0.001; Fig. 5D); pre-molt pups had a smaller proportion of blubber than molting (*P*=0.013) and post-molt pups (*P*=0.01). There was no difference in the proportion of blubber between molting and post-molt pups (Fig. 5D).

The top LMEs for each response variable are reported in Table 3. In all physiological parameter models, % blubber had the greatest positive effect on RMR (MR and msMR) in air and in water. Molt status and the interactions between molt and % blubber were also significant, though the negative effect of the interaction term lessened the effects. However, the random factor, individual ID, accounted for 30–40% of the variation (difference between conditional and marginal R^2). Dive parameters (fixed effects)

accounted for the variation (equal conditional and marginal R^2) models in water, however they accounted for little of the variation observed in air (Table 3). Mean dive depth was significant in all models; pups that dove deeper had lower RMR (MR and msMR) in both air and water, though the magnitude of the effect was greater in water than in air. Additionally, number of dives was significant in MR models in both treatments, though the effect was minimal.

DISCUSSION
Metabolic rates of wild seal pups in air and water across development
Metabolic rate measurement of large mammals is often conducted in captive situations where animals are trained, have time to acclimate to conditions, measurements can be randomized and/or repeated, and trial length depends on the animal's ability to perform trained behaviors (e.g. rest or hold in the case of swimming) (Dunkin et al., 2013; Liwanag, 2010; Liwanag et al., 2009; Rosen, 2021; Thometz et al., 2020; Williams et al., 1993). Whereas laboratory and captive settings are important for data collection in species for which wild measurements are not possible, these ideal conditions cannot be replicated in wild settings. This is especially true in the case of

Table 3. Results of the linear mixed effects models investigating relationships among physiological predictors and dive predictors relative to metabolic rate

Estimated parameter	Equation	AICc	△AICc	Weight	R^2 m (c)
Physiological parameters					
Air msMR ($\dot{V}_{O_2}$ min^{-1} kg^{-1})	−5.088+53.14(% blubber)+(molt status)+(molt status*% blubber)	89	19.66	1	0.44 (0.77)
Air MR ($\dot{V}_{O_2}$ min^{-1})	−308.6+1803.0(% blubber)+5.037(mass)+372.30(molt status)−1257(molt status*% blubber)	266.9	15.03	1	0.43 (0.82)
Water msMR ($\dot{V}_{O_2}$ min^{-1} kg^{-1})	4.952+18.59(% blubber)+4.933(molt status)− 17.66(molt status*% blubber)	72.9	4.21	0.886	0.27 (0.68)
Water MR ($\dot{V}_{O_2}$ min^{-1})	−585.6+3404.0(% blubber)+3.668 (mass)+ 649.00(molt status)−2040.00(molt status*% blubber)	207.7	63.92	1	0.25 (0.66)
Dive parameters					
Air msMR ($\dot{V}_{O_2}$ min^{-1} kg^{-1})	9.013−0.1243(mean depth)	88.2	6.1	0.906	0.14 (0.63)
Air MR ($\dot{V}_{O_2}$ min^{-1})	396.4+4.728(mass)−11.790(mean depth)+ 0.44070(mean duration)+1.505 (n dives)	253.8	2.21		0.15 (0.62)
Water msMR ($\dot{V}_{O_2}$ min^{-1} kg^{-1})	12.10−0.2698(mean depth)	81.8	8.65	0.98	0.55 (0.55)
Water MR ($\dot{V}_{O_2}$ min^{-1})	579.4+5.443(mass)−21.71(mean depth)	232.8	0.99	1	0.44 (0.44)
	570.4+5.64(mass)−21.93(mean depth)−0.3461(n dives)	233.8	2.6	1	0.42 (0.42)

The molt status coefficient should be multiplied by 0=pre-molt, 1=molting, 2=post-molt. ΔAICc is the difference in AICc between the top and 2nd ranked models.

young, dependent animals (Donohue et al., 2000; Rutishauser et al., 2004), as captive conditions do not represent the full range of challenges faced by young, growing seals.

During early development there can be many confounding factors that contribute to overall energy demand. For example, recorded air temperatures were warmer in weeks 5 and 7; although we expect that these warmer temperatures were likely within the TNZ for these pups. Among individual pups in this study, there were variable rates of development, and calendar age was not as important as developmental stage (i.e. blubber thickness and stage of molting) for metabolic rate. What causes variation in developmental rate is still unknown; although there was some variation in reproductive history and age, all pups in this study were born to multiparous mothers with the highest chances of successfully raising a pup to weaning (Hadley et al., 2007b; Proffitt et al., 2010). There are likely genetic influences that create variation in fitness (Chambert et al., 2014) and these differences may be related to rates of development, and thus variation in RMR, in pups (Burton et al., 2011). Burns and Testa (1997) also found a large amount of individual variation among pup physiology, despite controlling for as many factors as possible. We recognize that uncontrolled variables, combined with our relatively small sample size reducing the statistical power to detect differences among groups, makes it difficult to determine definitive contributions of multiple causative variables.

In this study, msMR$_A$ values were an average of 2.16 times Kleiber estimates of BMR for a terrestrial animal of similar mass, which is well within the reported range of RMR for phocid pups (Worthy and Lavigne, 1987), and similar to results of a previous study on Weddell seal pups (i.e. Elsner et al. (1977) reported RMR 1.5–2 times higher than predicted). MR$_A$ scaled with mass with a coefficient of 0.67, which follows the 2/3 scaling coefficient for basal MR (0.686±0.014; White and Seymour, 2003) and standard MR of euthermic mammals (0.675±0.013), but is slightly less than the interspecific scaling coefficient of thermoneutral RMR (0.712±0.013; White and Seymour, 2005). We did not detect any significant differences between animals that were lipemic and those that were not. Thus, we believe our measurements are good estimates of RMR for this species, and the observed variation is representative of natural variation within the population given the diverse developmental rates.

Typically, as mass increases, whole-animal metabolic rate increases allometrically. Contrary to this, MRs of Weddell seal pups were not allometric in water (Fig. 1); MR$_W$ measurements

were comparable between 7-week-old pups and 3-week-old pups (Fig. 2), although 7-week-olds were 1.5 times the mass of 3-week-old pups. Given that there was no significant difference in MR$_W$ by either age or molt status, and that T_C continued to be variable in all groups, this may represent a maximum thermal response of pups to submergence in water. Pups may direct their energy toward development of heat-saving mechanisms such as increasing insulation through blubber, or molting quickly, rather than reducing MR. For example, when we grouped pups by molt status rather than age, we saw that post-molt pups had a lower msMR$_W$ than pre-molt pups (Fig. 3B). Although there were no significant changes in thermal conductance across age in water, thermal conductance did decline when pups molted their lanugo (Table 2).

Similar to what has been reported for other species (Kvadsheim et al., 2005), we did not observe shivering during our water trials. In harp seal (*Pagophilus groenlandicus*) pups, shivering is suppressed during submergence regardless of core temperature but initiated in air when rectal temperature drops below 35.3±0.6°C (Kvadsheim et al., 2005). Weddell seal pups do shiver while hauled out (our unpublished data; Elsner et al., 1977; Ray and Smith, 1968), and there may be a similar T_C threshold in Weddell seals, though our results indicate it is likely below the lowest T_C measured in this study (34.2°C). Unlike harp seals, Weddell seal pups do not have brown adipose tissue (Elsner et al., 1977; Pearson et al., 2014b), so traditional non-shivering thermogenesis is not an option. Shivering is likely to be the mechanism that pups use to raise T_C after spending time in the water. Weddell seal pup skeletal muscle also has a much higher mitochondrial volume density compared with that in juveniles and adults, suggesting a role for mitochondria in thermogenesis (Kanatous et al., 2008).

Effect of molting

When pups were grouped by molt status (pre-molt, molting and post-molt), regardless of age or mass, a clearer pattern in RMR development emerged. Unlike for other phocid seals (Lavigne and Kovacs, 1988), molting does not appear to be tightly correlated with age in Weddell seal pups (our unpublished data). Pre-molt (those with lanugo) and molting pups had higher msMR than post-molt pups, and significantly different msMR between air and water, suggesting these pups are not thermally prepared to be in the water regardless of age. This is also true when MR is compared among molt status groups; only post-molt pups incurred the same metabolic costs in water as in air. Combined with the increased costs in water

for pre-molt and molting pups, these data suggest that Weddell seal pups experience little additional metabolic cost when in water after they have molted their lanugo. Therefore, to save energy, molting pups should spend the least amount of time in the water, but we observed the opposite; despite the increased metabolic costs, molting animals spent the greatest amount of time in the water (Fig. 4A). This energetic trade-off highlights the importance of spending time in the water when still dependent on their mother (Weitzner et al., 2021). Improved locomotor proficiency, stimulation of blubber deposition, cardiovascular conditioning for diving, and increased oxygen storage (i.e. increased myoglobin deposition) have all been shown to be drivers of increased submersion and diving in marine mammals (Ponganis, 2015) and are critical for developing pups, despite the thermal challenge submersion presents. Post-molt pups spent less time in the water, but this was likely because 6 of 7 post-molt pups in this study were weaned, and weaned pups spend less time in the water than dependent pups (Weitzner et al., 2021). Differences by molt status were independent of calendar age; thus, the faster a pup can molt, the sooner in-water RMR decreases. Increased RMR during molting is likely a result of increased heat loss in tandem with increased thermal conductivity of the pelage during that transitional stage. Previous research showed molting increased the conductivity of the fur layer of harp seals, resulting in higher rates of calculated heat loss for molting pups in air and water (Pearson et al., 2014a; 2019). Further, Boily (1995) showed that heat flux increases in molting phocids, especially in water. Molting has been shown to increase the RMR of several species of adult phocid, and the duration of the molt is directly related to the magnitude of the increase in RMR (Paterson et al., 2021; Thometz et al., 2020).

Thermoregulatory changes associated with molting and the subsequent effects on MR have also been observed during early development of otariid (eared) seals. Otariids have prolonged developmental periods compared with phocids, yet show similar patterns of MR development during dependency. Metabolic rate was more influenced by developmental stage and environment than calendar age in both northern fur seals (*Callorhinus ursinus*) and Antarctic fur seals (*Arctocephalus gazella*). Northern fur seal pups exhibited higher MR during the molt, which was especially pronounced in water (Donohue et al., 2000). Donohue et al. (2000) also describe a similar pattern in which pre-molt and molting pups had higher MR in water than post-molt pups, suggesting thermoregulatory development influences when northern fur seal pups enter the water. Antarctic fur seals had the lowest growth rates during molt, when pups were simultaneously spending more time in the water and regrowing pelage (McDonald et al., 2012). This suggests that otariids may also experience energetic trade-offs associated with the molt during development.

Core body temperature lability

Allowing core body temperature to fluctuate is a strategy employed by some endotherms to decrease the thermal gradient between the animal's core and the environment, thus reducing heat transfer (Bartholomew and Wilke, 1956; Costa and Kooyman, 1984; Donohue et al., 2000; Levesque et al., 2016). This may be especially important for smaller-bodied mammals in seawater, owing to high surface area to volume ratios and the high thermal conductivity of water. Contrary to our hypothesis, we observed a small drop in T_C in water in all age groups and molt groups for Weddell seal pups, which suggests that even though RMR was equivalent between air and water for post-molt pups, there may still some cost to being immersed. Non-molting animals, regardless of whether they had lanugo or juvenile fur, were better able to maintain

a T_C in air than molting pups, as non-molting animals showed little decline in T_C in air (and a similar decline in T_C to molting animals in water), whereas molting animals showed a similar decline of T_C in air and in water. This is likely due to the need to perfuse the skin for molting. In water, molt status did not matter, and pups at all time points showed a similar decrease in T_C; pups at 3 and 5 weeks of age had a similar decrease in air as in water.

Lowering T_C may be one mechanism pups use to slow heat loss by extending a temperature gradient deeper into tissues, similar to harp seal pups in water (Worthy, 1991); alternatively, this may be a passive decline in T_C as a result of decreased blood flow to muscle and accessory organs during the dive response (Zapol et al., 1979). All comparative groups in this study (age, molt status) had similar drops in T_C in water, indicating this did not contribute to differences in thermal conductance, but rather differences in conductance were due to differences in RMR among groups. Mass gain also likely contributed to the reduction in the thermal conductance of pups with age, as increasing mass decreases their surface area to volume ratio; thermal conductance was highest in 1-week-old pups, which had a comparatively small body size, little blubber and lanugo coats. In water, all pups had equivalent MR, regardless of molt status. It may be that the 0.5°C drop in T_C is not enough to confer much energetic savings, as there was no significant difference in thermal conductance between the beginning of a trial and the end of a trial when T_C had declined. Our results are different from those reported for Weddell seal pups by Elsner et al. (1977), who did not observe any drop in T_C in air or water trials when pups were more than 9 days old. Time of immersion was similar in both instances (~35 min). Neither the former nor present study observed pups shivering while in the water.

The lability of body temperature in all groups in water indicates that Weddell seal pups may not be within their TNZ while in sea water at −1.8°C. Alternatively, dropping body temperature may be a strategy employed by Weddell seals to reduce heat loss, which decreases MR and thus oxygen consumption, prolonging dive time. It is unclear whether this strategy is employed by adult Weddell seals; aortic temperature drops of 2°C have been observed during dives (Kooyman et al., 1980; Hill, 1987), whereas Ponganis et al. (1993) reported decreases in muscle temperature of less than 1°C soon after water entry. We observed similar changes in core temperature in this study, suggesting that minor fluctuation in body temperature while in the water may be a typical strategy for Weddell seals.

Respiratory exchange ratios (RER)

Respiratory exchange ratio (RER) provides an indication of metabolic fuel sources (Elia and Livesey, 1988; Ferrannini, 1988). In this study, calculated RER indicated that Weddell seal pups are using a mix of lipids and protein or carbohydrate throughout dependency. Previous work has shown Weddell seal milk has very little carbohydrate (Eisert et al., 2013). Accordingly, pups are likely relying on a mix of lipids and proteins as fuel. An RER>1 indicates lipid deposition (Elia and Livesey, 1988; Ferrannini, 1988); observed values greater than 0.8 likely signal a mix of using lipid for fuel and depositing lipid in blubber. We saw differences in RER between dependent and independent pups (Table 2): dependent pups had an average RER of 0.925, suggesting both lipid deposition and lipid burning, whereas independent pups' mean RER was lower at 0.788 (and much less variable), supporting our hypothesis of mixed lipid and protein fuel use, with little or no lipid deposition. These values are higher than RER values reported by Elsner et al. (1977; RER=0.76); however, pups in that study were fasted for 4 h

before RMR measurements. Mixed fuel use (lipid and protein) during submergence is also seen in other species while fasting (e.g. harp seals; Worthy and Lavigne, 1987). Using protein as fuel in addition to lipid helps preserve the blubber layer, preserving insulation when in water.

While Weddell seals do not undergo a typical 'post-weaning fast' observed in other phocid species (Arnbom et al., 1993; Noren and Mangel, 2004; Bennett et al., 2010; Reiter et al., 1978; Worthy and Lavigne, 1983; 1987), there is no evidence that they begin feeding while dependent or soon after weaning (Burns and Testa, 1997; Rea et al., 1997; Sato et al., 2003; Weitzner et al., 2021). During the transition to independence, Weddell seals may burn a mix of lean tissue and blubber to preserve the blubber for insulation, similarly to harp seals (Worthy and Lavigne, 1987). Habitat use (ice and water versus land and water) has been shown to affect the preferred energy source while fasting (Worthy and Lavigne, 1987); however, habitat use (both ice and water) is similar between dependent and independent Weddell seals. Although we did not find a statistically significant difference in RER between dependent and independent pups, independent pups had a mean RER similar to that reported for harp seals (Table 2; Worthy and Lavigne, 1987).

Influence of body composition and dive behavior on metabolic rates

As proportion of total blubber (% blubber) increased, so did both MR and msMR, which is expected given the increase in mass that accompanies increasing blubber. This relationship is not exact, though, as shown by the much larger effect of blubber than mass on MR (Table 3). Although blubber is typically considered to be a low metabolic activity (inert) tissue in adults (Strandberg et al., 2008; Favilla et al., 2021), growing pups are actively depositing lipids into adipose tissue, creating internal structure during the entire nursing period (Dunkin et al., 2005; Pearson et al., 2014b; Struntz et al., 2004), eventually resulting in the stratified structure of adult blubber (Liwanag et al., 2012b; Wheatley et al., 2007). This likely results in nearly constant blood flow to the entire blubber layer during development. Our results suggest the tissue is metabolically active, and thus contributes to increased RMR. This may change after weaning, when pups preserve energy stores (blubber) before they successfully forage.

Mixed models showed that dive parameters (i.e. dive experience) do not appear to influence development of MR in this species. The strongest model indicated a negative relationship between dive depth and MR, such that animals with lower MR dove deeper. This is likely a result of a lower MR extending oxygen store use rates, which is an expected strategy as part of the mammalian dive response. Pups with naturally low MR may be at an advantage as they are able to dive deeper and possibly longer than pups with higher MR. Although mean dive time did not have a significant influence on MR, there was ample variation in dive times amongst pups (Weitzner et al., 2021), and mean duration might not be the best metric of experience. Mean dive duration of 2.38 min reported in Weitzner et al. (2021) was well below the calculated aerobic dive limit for this species (4–5 min; Burns and Castellini, 1996). Pups spend the largest proportion of their time in the water swimming at the surface (39.3% of dives are shallower than 5 m), gaining experience in the water, rather than performing deep dives (Weitzner et al., 2021).

Whereas many species of pinniped experience broad ranges of water temperatures (~15°C range) and must be able to thermoregulate across the range (Donohue et al., 2000; Liwanag,

2010; Rosen and Trites, 2013), the Southern Ocean is comparatively stable at −1.8±1°C, with little thermocline (Hunt et al., 2003). Thus, Weddell seal pups will not experience much colder water temperatures than they experienced in the RMR trials in this study, even at depth. As such, the metabolic rates in water reported in this study are likely maximal metabolic rates (energy expenditure) in water.

Conclusion

It has been suggested that pinniped pups forego metabolically costly activities, such as swimming and diving, to maximize the energy available for growth and storage before weaning, as energy storage is more beneficial for survival than gaining dive capacity and foraging skills (Bennett et al., 2010; Noren and Mangel, 2004). However, the results of this study indicate that developing pups do not sacrifice swimming or diving to maximize energy storage. Our results support our hypothesis that Weddell seal pups experience an energetic trade-off during the dependency period. Pups must balance staying hauled out, reducing thermoregulatory costs and thus lowering RMR to conserve energy for development, versus entering the water to develop swimming and diving skills (Weitzner et al., 2021) and diving physiology, which results in increased RMR to thermoregulate. Additionally, molting and growth further complicate the energetic demands of young pups. This energetic trade-off is especially pronounced when pups are actively molting, yet despite the increased energetic cost, our results show molting pups spend the greatest amount of time in the water. Additionally, molt status was more important than calendar age or mass in determining RMR. If climate change causes reductions in sea ice as predicted (Parkinson, 2019), young, pre-molt and molting pups may face greater metabolic costs if forced into the water too early because of unstable ice conditions or early break-out of the fast ice. Mass gain is directly linked to survival to weaning and first-year survival (Hill, 1987; Mannas, 2011; Proffitt et al., 2008), but it may be that molt timing and duration are also linked to first-year survival. Pups that molt early or faster may be at an advantage, but it is unclear how this affects survival after weaning and first-year survival in this species. Future studies should investigate the speed and timing of the molt, and track pups through their first year to elucidate these relationships.

of Science and Mathematics at California Polytechnic State University, San Luis Obispo.

Data availability

Data are publicly available at the U.S. Antarctic Program Data Center (USAP-DC): https://www.usap-dc.org/.

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