Research article

Intrinsic and extrinsic influences on standard metabolic rates of three species of Australian otariid

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The study of marine mammal energetics can shed light on how these animals might adapt to changing environments. Their physiological potential to adapt will be influenced by extrinsic factors, such as temperature, and by intrinsic factors, such as sex and reproduction. We measured the standard metabolic rate (SMR) of males and females of three Australian otariid species (two Australian fur seals, three New Zealand fur seals and seven Australian sea lions). Mean SMR ranged from 0.47 to 1.05 l O_2 min^{-1}, which when adjusted for mass was from 5.33 to 7.44 ml O_2 min^{-1} kg^{-1}. We found that Australian sea lion mass-specific SMR (sSMR; in millilitres of oxygen per minute per kilogram) varied little in response to time of year or moult, but was significantly influenced by sex and water temperature. Likewise, sSMR of Australian and New Zealand fur seals was also influenced by sex and water temperature, but also by time of year (pre-moult, moult or post-moult). During the moult, fur seals had significantly higher sSMR than at other times of the year, whereas there was no discernible effect of moult for sea lions. For both groups, females had higher sSMR than males, but sea lions and fur seals showed different responses to changes in water temperature. The sSMR of fur seals increased with increasing water temperature, whereas sSMR of sea lions decreased with increasing water temperature. There were no species differences when comparing animals of the same sex. Our study suggests that fur seals have more flexibility in their physiology than sea lions, perhaps implying that they will be more resilient in a changing environment.

Key words: Metabolic rate, otariid, sex, water temperature

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Introduction

Predicted global climate change is already altering the marine environment and will subsequently affect the animals that live and hunt within its bounds (Simmonds and Isaac, 2007). Some of the changes expected include increasing ocean temperatures and changes to seasonal oceanic processes that will be likely to affect the distribution of fish assemblages within the marine environment (Learmonth *et al.*, 2006; Schumann *et al.*, 2013). Pinnipeds may be particularly susceptible to these changes if their prey distribution alters such that they have to travel further or dive deeper to obtain food (Staniland *et al.*, 2007) or if the marine environment warms to such an extent that they cannot thermoregulate effectively

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(Boyles *et al.*, 2011). Thus, in order to predict how changes in environmental conditions might impact on pinnipeds it is important to understand how different groups use their energy stores over a range of environmental conditions (Canale and Henry, 2010). Understanding how much flexibility pinnipeds have in order to adapt to the changing conditions can be, in part, met through studying their energetics (Geiser and Turbill, 2009; Canale and Henry, 2010).

The study of energetics provides information about the needs of pinnipeds and the cost of satisfying those needs (Williams and Yeates, 2004). Survival requires the maintenance of an overall positive energy balance, satisfied by obtaining more energy than is expended. Energy expenditure is most accurately estimated by determining metabolic rates, and these can vary over seasons and years, with body mass accounting for most of this variation for mammals (Kleiber, 1947; McNab, 2008). Pinniped energy expenditure is also influenced by intrinsic factors, such as activity, reproduction (preparation for and recovery from the energetic demands of the breeding season), moult and sex, and extrinsic factors, such as temperature and photoperiod, can also contribute to some of this variation. These factors have been investigated in a wide range of phocid (e.g. Rosen and Renouf, 1995; Boily and Lavigne, 1997; Ochoa-Acuña *et al.*, 1998; Sparling *et al.*, 2006) and otariid seals (e.g. Costa and Gales, 2003; Williams *et al.*, 2007; Ladds *et al.*, 2016) but have not shown any consistent relationships among species.

Harbour seals (*Phoca vitulina*) demonstrate sex and age variation, with metabolic rates declining with age, females faster than males, and they experience metabolic depression during pre- and post-moult stages (Rosen and Renouf, 1995). In contrast, grey seals (*Halichoerus grypus*) have their highest metabolic rate during winter and they increase, rather than depress, their metabolic rate during the moult (Boily and Lavigne, 1997). Within otariids there appear to be clear seasonal patterns in metabolic rate of fur seals (Dalton *et al.*, 2015), although no effect of reproduction or season has been found for sea lions (Williams *et al.*, 2007). The processes that underlie these variations in response to changing environmental conditions are not well understood, and it is clear that the responses vary greatly between and within pinniped species.

Fur seals and sea lions differ greatly in their thermoregulatory strategies. Fur seals rely on two thick layers of fur to thermoregulate, trapping a layer of air between their fur layers to support its insulation (Liwanag *et al.*, 2012a). The fur seal blubber layer is metabolically inert and is primarily used for energy storage (Liwanag *et al.*, 2012a; Dalton *et al.*, 2014a). Sea lions, on the other hand, rely on a thick blubber layer interspersed with layers of muscle (Mellish *et al.*, 2004) to protect themselves from cold water (Mellish *et al.*, 2007; Williams *et al.*, 2007; Liwanag *et al.*, 2012b). Sea lions maintain two blubber layers, one for energy storage, which maintains a constant thickness throughout the year, and one for

thermal insulation, which responds to changes in temperature (Williams *et al.*, 2007).

The three otariid species that occupy Australian waters present an interesting comparison of how marine mammals may respond to ecosystem changes, as they have different reproductive cycles, thermoregulatory methods and foraging strategies. The Australian fur seal (*Arctocephalus pusillus doriferus*) and the New Zealand fur seal (*Arctocephalus forsteri*) have an annual breeding and moulting cycle typical of pinnipeds (Fig. 1; Goldsworthy and Shaughnessy, 1994; Gibbens and Arnould, 2009). In contrast, the Australian sea lion (*Neophoca cinerea*) breeds asynchronously every 17–18 months (Higgins, 1993; Gales *et al.*, 1994) and has an extended moult that can occur at any time of the year. Both the Australian fur seal (Arnould and Hindell, 2001; Kirkwood *et al.*, 2006) and the Australian sea lion are predominantly benthic foragers (Costa and Gales, 2003; Lowther *et al.*, 2013), whereas the New Zealand fur seals are typically pelagic foragers (Harcourt *et al.*, 2002).

The habitats of the Australian fur seal and the Australian sea lion do not overlap, but the New Zealand fur seal occurs across both the feeding and breeding ranges of the other two species (Page *et al.*, 2005a; Campbell *et al.*, 2014). The ranges of the Australian fur seal and the New Zealand fur seal are currently expanding as they begin to reoccupy territory they held before commercial sealing (Goldsworthy *et al.*, 2003), whereas the Australian sea lion is listed as endangered, and the population continues to decline (McIntosh *et al.*, 2013). By investigating how marine mammals occupying similar habitats but using different reproductive and foraging strategies vary their primary energy expenditure over the course of a year, we can begin to understand how they might respond to environmental changes. Therefore, it was the aim of this study to explore the intrinsic and extrinsic influences on metabolic rate in a sample of fur seals and sea lions.

Materials and methods

Animals

We conducted experiments to measure the metabolic rates of captive otariids (*n* = 12) in three Australian marine facilities: Dolphin Marine Magic, Coffs Harbour (RF1: 30°17′S, 153° 8′E); Underwater World, Sunshine Coast (RF2: 25°40′S, 153°7′E); and Taronga Zoo, Sydney (RF3: 33°50′S, 151°14′ E). Experiments were conducted at various times of year from 2013 to 2015. Owing to logistical constraints, it was not possible to measure all otariids in the same month of the same year (data collection periods are shown in Fig. 1). Rather, for fur seals we ensured that sampling was spread over the year but included each significant stage of their annual cycle (analogous to moult, post-moult and prior to the moult, but before breeding; Fig. 1). Australian sea lions were measured at the same time as the fur seals because we could not determine their moulting and breeding cycles.
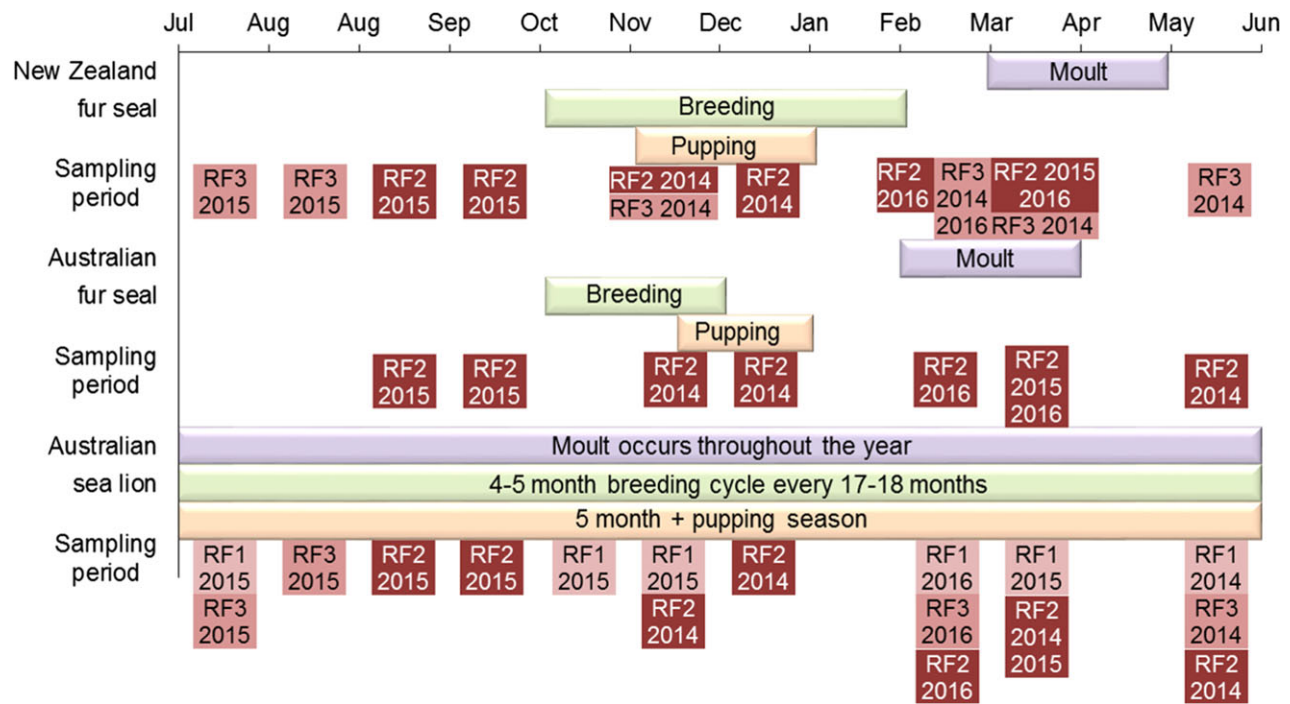
Figure 1: Moulting, breeding and pupping time line of Australian fur seals, New Zealand fur seals and Australian sea lions and timetable of experiments conducted at three Australian marine facilities over 3 years. Shaded boxes indicate that trials were conducted during that month in the respective facility. RF1 is located in a temperate to sub-tropical region, RF2 is located in a sub-tropical region, and RF3 is located in a temperate region.

During each visit to the marine facility, the animals were measured between one and four times. We used three New Zealand fur seals, two Australian fur seals and seven Australian sea lions, all of which were not reproducing at the time of experiments, were on permanent display at their respective facilities and were cared for under the husbandry guidelines of that facility. The study was approved by Macquarie University ethics committee (ARA-2012_064) and Taronga Conservation Society Australia ethics committee (4c/10/13). All Australian sea lions that participated in the study were born as a part of an ongoing captive breeding programme in Australian aquaria, whereas all fur seals came into captivity as juveniles after having been found in poor health or injured and were considered unsuitable for release back into the wild after rehabilitation. Fur seal ages were estimated from their size and condition when they were introduced to their facility, and they are now all subadults or adults. Otariids were weighed once per week as a part of their normal routine.

Metabolic rate measurements

We measured the standard metabolic rate (SMR) of otariids using open-flow respirometry. Standard metabolic rate was used because otariids were measured in water and they did not adhere to all of the standards of Kleiber for measuring basal metabolic rate (Kleiber, 1975; Hurley and Costa, 2001).

Otariids had not fed for at least 10 h before each trial to ensure they were post-absorptive (Rosen and Trites, 1997), and no animals were pregnant or lactating. Otariids were quiescent (not sleeping) during measurement and reached steady-states of oxygen consumption in 5 min or less. Otariids were measured early in the morning, before they had become active (i.e. swimming), and participated in trials only if they were found to be dry in their enclosure. Measurements of metabolic rate were recorded for up to 15 min, with the lowest, consistent 3 min (minimum) being used for analysis.

We measured SMR when otariids were sitting upright and still in water under a moulded acrylic hood (80 litres). This behaviour was reinforced with small amounts of food (fish and squid), which were reduced as each otariid's capacity to remain inactive improved with training. This amount of food would not have influenced metabolic rate (Rosen and Renouf, 1997; Rosen et al., 2015). The hood was connected to an open-flow respirometry system (Sable Systems International, Inc., Henderson, NV, USA), where air was pulled from the hood with a Sable Systems Mass Flow pump at an adjustable flow rate ranging from 300 to $350 \, l \, min^{-1}$. We adjusted and monitored the flow for each individual to ensure that the oxygen inside the hood remained >20%. A continuous sub-sample was drawn into the analyser from the pump at ~1200 ml min^{-1}, pushed through the analyser and measured for water vapour then dried (magnesium

perchlorate) and scrubbed of carbon dioxide (soda lime) before entering an FC-1 oxygen analyser. We monitored the scrubbers using the built-in CO_2 analyser and an external water vapour analyser for fluctuations above 1 and 5%, respectively. The percentage of oxygen in the expired air was measured continuously with Sable Systems ExpeData software and recorded at five samples per second. Oxygen consumption was calculated using equations from Withers (1977), assuming a respiratory quotient (RQ) of 0.77 (Feldkamp, 1987; Boyd et al., 1995b).

We calibrated the system every 2–3 days using nitrogen (N_2) and ambient air, following the method of Fedak et al. (1987). Nitrogen gas was passed through a flowmeter at a known rate using a Sable Systems FoxBox. The predicted values of the N_2 flow were 400 and 500 ml min^{-1}. Values were within ±5% of predicted values.

Analyses

Before analysis, we examined the suitability of the data for analysis using linear models. We used a linear regression to investigate the relationship between mass (in kilograms) and SMR (in litres of oxygen per minute). Owing to the large range, mass was logarithmically transformed, and we used mass-specific SMR (henceforth, sSMR; in millilitres of oxygen per minute per kilogram) to make statistically relevant comparisons across fur seal and sea lion groups. We identified outliers in the continuous response variables (SMR and sSMR) using exploratory graphical techniques and removed any that corresponded to a behavioural anomaly. We also assessed collinearity-correlation among explanatory variables [mass, sex, age, moult (presence/absence), animal identity, month, ambient temperature and water temperature] via multiple pair-wise scatterplots (pair plots; Zuur et al., 2009b, 2010). We examined the response variables for normality visually using a histogram, and any factor explanatory variables were tested for equal variances across the response variable (Bartlett's test).

We measured the metabolic rate of a subset of six otariids (NFM1, AFM1, ASM2, ASF2, ASF3 and ASF5) in the same month, 1 year apart and used Student's paired t-tests to look for differences in mean sSMR in order to test for a training effect. As there were no significant differences ($P > 0.05$) in mean sSMR for any of the six otariids between the two years, training effects were not considered further.

Fur seal and sea lion sSMR data were analysed separately. We used multiple linear mixed-effects models (LME) with restricted maximum likelihood (REML) estimation to evaluate which sources of variation best explained changes in sSMR (in millilitres of oxygen per minute per kilogram; NLME package in R; Pinheiro et al., 2014). Using sSMR as the response variable, we first ran a null model (no random effects) to find a baseline from which we could evaluate the influence of the random effect on the models. We then ran LMEs with animal identity as the random effect to account

for repeated measures. The predictor variables for sea lions were as follows: sex, age, month of the year, moult (absence/presence) and water temperature. We did not use ambient temperature in the models as it was highly collinearly related to water temperature, which was used in preference because the animals were measured in the water. As month is a cyclical variable, we transformed it to sine [sin(360/11) × month] or cosine [cos(360/11) × month], as in the study of Sparling et al. (2006), and both were tested in the model. The predictor variables for fur seals were as follows: sex, age, species, season (pre-moult, moult, post-moult) and water temperature. We chose to use an information-theoretical approach to build candidate models because stepwise model selection can produce unreliable results (Whittingham et al., 2006). The models were run with all combinations of predictor variables using dredge from the R package MuMIn (Bartoń, 2013). Models were ranked using 'model.sel' from the R package MuMIn, and Akaike model weights were used to rank the models.

Model selection was based on a combination of Akaike information criteria (AICc), log likelihoods (logLik) and R^2. The amount of variance explained by the random effect was assessed through the difference of the marginal (fixed effect only) and conditional (all model variables) R^2 (rsquared. glmm function). The assumptions of homoscedasticity, normality, homogeneity and independence were investigated by plotting predicted vs. fitted residuals, QQ-plots, Cleveland dot-plots and ACF plots (Zuur et al., 2009a). Where possible, we tested for significant differences in sSMR and factorial predictor variables across classes of otariids using a *post hoc* general linear hypothesis and multiple comparisons test via the Tukey method with the function glht from the package multcomp (Hothorn et al., 2013). All analysis was completed in R (version 3.1.3; R Core Development Team, 2015), and values are reported as means ± SD.

Results

Metabolic rates measured at rest in water were collected for 12 otariids at semi-regular intervals over 3 years (Fig. 2). A total of 155 measurements were collected, with 153 used for analysis because two observations were excluded as they were identified as outliers from behavioural anomalies. There was a strong positive relationship between SMR (in litres of oxygen per minute) and log mass (in kilograms) for all 12 otariids expressed by the following equation: log (SMR) = −3.48 + 0.66log(mass) (logLik = 57.78, $R^2 = 0.769$, $P < 0.001$; Fig. 2). The mean SMR for all otariids ranged from 0.34 to 1.311 O_2 min^{-1}, and sSMR ranged from 3.06 to 9.71 ml O_2 min^{-1} kg^{-1} (Table 1).

Fur seals

Australian fur seals and New Zealand fur seals have an annual moult and breeding season that occur at similar times of year (Fig. 1). The model that best explained the variation

in sSMR for fur seals included an interaction between season (pre-moult, moult or post-moult) and sex, and there was a large effect of animal identity [LME: AICc = 154.8; logLik = −69.38, R^2 (conditional) = 0.267; R^2 (marginal) = 0.839]. There was no significant effect of age, water temperature or species. The sSMR for both males and females was lowest during post-moult (Fig. 3). For males, sSMR was highest during the annual moult, whereas for females the sSMR was highest during the pre-moult (Fig. 3). Although season was able to explain more of the variance in the model than water temperature, there was a positive linear relationship between water temperature and sSMR for each of the four fur seals (Fig. 4A–D).

Sea lions

Australian sea lion moult and breeding can occur at any time of the year, so it was not possible to examine the effect of season on metabolic rate. Instead, we tested the effect of sine and cosine of month. The final model for sea lions included water temperature and sex as fixed effects, with individual as the random effect. Animal identity had an effect on the model, as the variance explained was improved [LME: AICc = 281.0, logLik = −134.01, R^2 (conditional) = 0.284, R^2 (marginal) = 0.515]. Females had higher sSMR than males (Fig. 5), although sine month, cosine month, moult and age did not contribute to the final model. Sea lions housed at RF1 and RF3 were exposed to a wide range of water temperatures (16–27°C), and there was a negative relationship between sSMR and water temperature (Fig. 6A–D). Sea lions from RF2 were measured in water temperatures of 22–27°C, but there was no relationship between sSMR and water temperature.

Discussion

Standard metabolic rate

Measuring pinnipeds in captivity provides an excellent proxy for estimating the energy expenditure of wild populations. Respirometry is considered the most accurate method of measuring metabolic rate, but is inherently difficult to use in the wild (Boyd, 2002; Halsey *et al.*, 2009; Dalton *et al.*, 2014b). Therefore, these types of experiments allow us to develop our understanding of the physiology of target species, with minimal impact on populations and using the most accurate technology available. We measured the SMR of three species of otariid (n = 12) at rest in water during significant times of their annual cycle. We found that the mean sSMR for the otariids in this study were 2–2.2 times (Table 1) that predicted by Kleiber (1975), which falls within the range predicted for a marine mammal (Williams *et al.*, 2001) and is lower than the in-air resting metabolic rate of juvenile northern fur seals (2.9 times predicted; Dalton *et al.*, 2015) and than the average daily metabolic rate of lactating northern fur seals (3.2 times predicted; Costa and Gentry, 1986).
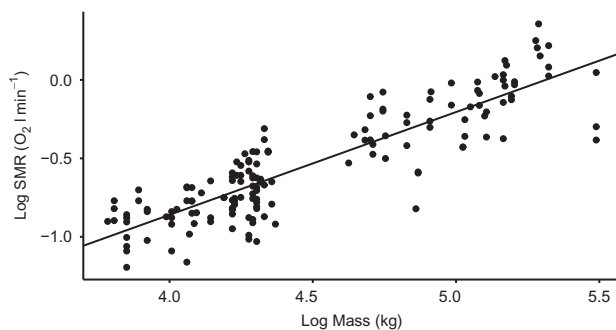

Figure 2: Logarithm of metabolic rate while resting in water (SMR; in litres of oxygen per minute) as a function of the logarithm of body mass (in kilograms) for one female Australian fur seal (n = 13), one male Australian fur seal (n = 16), three male New Zealand furseals (n = 31), five female Australian sea lions (n = 68) and two male Australian sea lions (n = 26). The line plotted is the fitted equation: log(SMR) = −3.48 + 0.66log(mass).

Table 1: Mean ± SD of standard metabolic rate (in litres of oxygen per minute) and mass-specific standard metabolic rate (in millilitres of oxygen per minute per kilogram), multiples of basal metabolic rate and the age, mass range and sample sizes for Australian fur seals, New Zealand fur seals and Australian sea lions

Species and sex	n	Age range (years)	Mass range (kg)	Total trials	SMR (l O$_2$ min^{-1})	sSMR (ml O$_2$ min^{-1} kg^{-1})	BMR multiple
Australian fur seal							
Female	1	17.8–19.1	69–79	13	0.49 ± 0.06	6.63 ± 1.04	2.0
Male	1	15.1–17.1	175–242	16	1.05 ± 0.20	5.33 ± 1.18	2.1
New Zealand fur seal							
Male	3	7.5–14.0	47–161	31	0.62 ± 0.18	6.42 ± 1.66	2.2
Australian sea lion							
Female	5	5.1–26.4	44–76	68	0.47 ± 0.08	7.44 ± 1.16	2.1
Male	2	9.0–14.3	108–177	25	0.84 ± 0.13	5.94 ± 1.09	2.0

Abbreviations: BMR, basal metabolic rate; SMR, standard metabolic rate; sSMR, mass-specific standard metabolic rate.

Few studies have successfully measured the true basal metabolic rate of pinnipeds in the strict conditions of Kleiber (1975). The captive otariids were adult, non-reproductive, quiescent and post-absorptive, but they were measured for a relatively short time and in water. We measured captive otariids in the morning, before they became active, and only if they were dry, suggesting that they had been resting and not swimming before measurement. We measured them in water because they were habituated to this experimental set-up and were noticeably calm during experiments, corresponding to their relatively low metabolic rate, despite not meeting all of the conditions of Kleiber (1975). The range of average sSMR for the animals in this study was 5.3–7.4 ml O_2 min^{-1} kg^{-1}, which was within the range of resting metabolic rate from Southern sea lions (*Otaria flavescens*) of a similar size (4.3–9.1 ml O_2 min^{-1} kg^{-1}; Dassis *et al.*, 2012). In that study, a single captive animal had resting metabolic rate within the range of the wild animals that were measured simultaneously. We therefore consider our results to be a good estimate of resting metabolic rate in these species, and our measurement of sSMR is probably approaching basal metabolic rate.
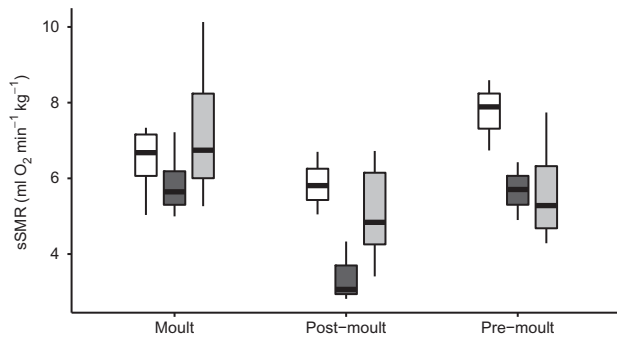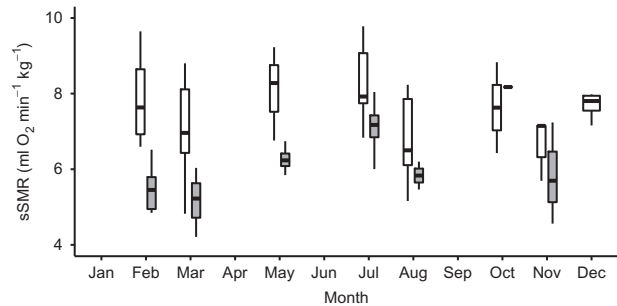

Figure 3: Median, interquartile range (box) and range (bars) of mass-specific standard metabolic rate (sSMR; in millilitres of oxygen per minute per kilogram) for an Australian fur seal male (black box, $n = 1$) and female (white box, $n = 1$) and New Zealand fur seal males (grey box, $n = 3$) during the moult, post-moult and pre-moult periods.

Figure 4: Median, interquartile range (box) and range (bars) of mass-specific standard metabolic rate (sSMR; in millilitres of oxygen per minute per kilogram) for male (grey box, $n = 2$) and female (white box, $n = 5$) Australian sea lions over the course of the year.

Influence of the annual cycle on metabolic rates

The stages of the annual cycle that are energetically costly for otariids are the preparation for and the recovery from annual breeding, including the annual moult. Thus, it is expected that the moult and breeding will have the greatest influence on the variation in the metabolic rate of pinnipeds (Costa and Trillmich, 1988; Rosen and Renouf, 1995). Australian sea lions have different reproductive and moulting strategies from every other otariid, whereas the Australian fur seal and New Zealand fur seal have typical yearly cycles of pinnipeds. Australian fur seals and New Zealand fur seals are similar, with breeding and pupping occurring during the Austral summer, followed by a moult (Goldsworthy and Shaughnessy, 1994; Gibbens and Arnould, 2009). In contrast, Australian sea lions have an asynchronous breeding and moulting cycle, where females come into oestrus every 17–18 months and moulting can occur year round for 3–4 months (Higgins, 1993; Gales *et al.*, 1994). This lack of synchronization was evident in the sSMR of the sea lions, as there were no significant changes over the course of the year, whereas fur seals had distinct changes in their sSMR coinciding with the moult and the build-up of body condition before the breeding season.

Fur seals

In the preparation for and recovery from breeding, male and female fur seals have different motivations for fat
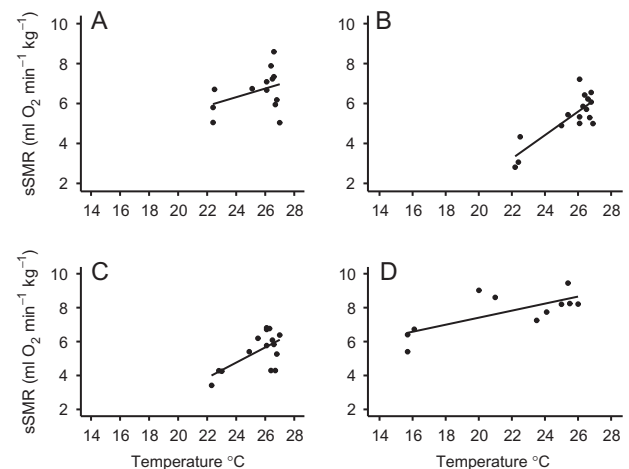

Figure 5: Relationship between mass-specific standard metabolic rate (sSMR; in millilitres of oxygen per minute per kilogram) and water temperature (WT; in degrees Celsius) for four individual fur seals. (**A**) Female Australian fur seal (sSMR = 1.12 + 0.21 × WT, logLik = −17.42, R^2 = 0.140, P = 0.207, n = 13). (**B**) Male Australian fur seal (sSMR = −9.70 + 0.59 × WT, logLik = −15.63, R^2 = 0.683, $P < 0.001$, n = 16). (**C**) Male New Zealand fur seal (sSMR = −5.99 + 0.45 × WT, logLik = −18.36, R^2 = 0.404, P = 0.011, n = 15). (**D**) Male New Zealand fur seal (sSMR = 1.95 + 0.29 × WT, logLik = −14.70, R^2 = 0.587, P = 0.003, n = 12).
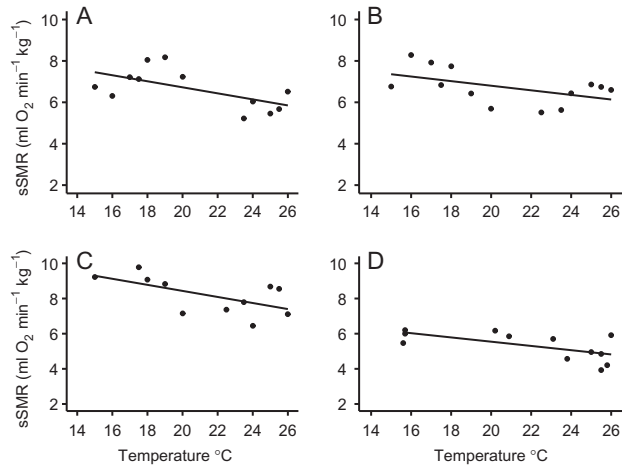
Figure 6: Relationship between mass-specific standard metabolic rate (sSMR; in millilitres of oxygen per minute per kilogram) and water temperature (WT; in degrees Celsius) for Australian sea lions. (**A**) Adult male (ASM1; sSMR = 9.79 − 0.16 × WT, logLik = −12.40, R^2 = 0.450, P = 0.017, n = 12). (**B**) Adult female (ASF4; sSMR = 9.26 − 0.12 × WT, logLik = −13.16, R^2 = 0.348, P = 0.034, n = 13). (**C**) Adult female (ASF2; sSMR = 12.67 − 0.20 × WT, logLik = −14.38, R^2 = 0.497, P = 0.011, n = 12). (**D**) Adult male (ASM2; sSMR = 7.96 − 0.12 × WT, logLik = −11.73, R^2 = 0.336, P = 0.038, n = 13).

accumulation, although their physiological responses appear similar. Females allocate their energy resources to fat stores for gestation and milk production that must be maintained year round if the female is pregnant or lactating (Costa, 1991). Females are usually pregnant during the pre-moult period and must be in good condition to birth and feed a new pup (Boyd et al., 1995a). Females in better condition more often give birth to larger pups that have a higher chance of survival (Guinet et al., 1998). Dominant males require a large body mass during the breeding season in order to establish and defend territory and reproduce successfully, whereas during the non-breeding season they generally maintain a lower body mass when they leave the breeding areas to forage (Boyd and Duck, 1991; Carey, 1991). This is an energetically costly endeavour that only large, healthy males can achieve (Boyd and Duck, 1991). We found that the rate of energy expenditure from male and female fur seals was consistent with that expected for wild fur seals (Costa and Gentry, 1986). Male sSMR was highest during the moult and lowest during the post-moult, after which it increased again before the breeding season. In females, resting metabolic rate was much more consistent, increasing from the post-moult (lowest) to the pre-moult (highest). These metabolic changes align with body conditions of wild Australian fur seals, where the blubber distribution of females does not change over the course of the year, whereas males undergo large seasonal shifts (Carey, 1991; Arnould and Warneke, 2002).

We found that for both fur seal species, sSMR was the lowest during the post-moult (Austral autumn and winter)

period. The reduction in sSMR during this period is likely to be a strategy to maintain body condition during periods of reduced prey availability and increased thermoregulatory demands. For both fur seal species, the post-moult period corresponds to the lowest sea-surface temperatures and, presumably, the time of lowest productivity within their home ranges (Harris et al., 1991; Baylis et al., 2008b). Lactating Australian and New Zealand fur seals tend to undertake their longest foraging trips (Arnould and Hindell, 2001; Harcourt et al., 2002; Page et al., 2005b; Baylis et al., 2008a; Kirkwood and Arnould, 2011) and seals tend to maintain a lower body mass (corresponding to a low metabolic rate) after the moulting and breeding season (Arnould and Warneke, 2002; Beck et al., 2003; Sparling et al., 2006).

Sometime before the breeding season, male fur seals increase their metabolic rate from the post-moult period (Fig. 3). The female Australian fur seal also showed an increase, although not as pronounced as for males. It may be important that this event is synchronized for males and females such that they reach sexual maturity simultaneously each year (Boyd, 1991). The timing also corresponds to the accumulation of fat; as the fur seals get fatter, their metabolic rate increases (Beck et al., 2003). As we were unable to measure the fur seals year round, the exact timing of this phenomenon is unknown, although it is likely to be consistent with the onset of spermatogenesis for males, which begins 3–4 months before the breeding season (Stewardson et al., 1998; Stewardson, 2007). Spermatogenesis is energetically expensive, particularly for large mammals with low metabolic rates (Gomendio et al., 2011).

Males and females have different energy requirements at different times that can be achieved by either eating more or reducing energy use. Our results demonstrate that fur seals decrease their energy use during times of fat accumulation, and anecdotal evidence from captivity suggests that the quantity of food increases during this time for fur seals (A. Tolley, M. Ryan and R. Tate, personal communication). In the wild, New Zealand fur seals target higher-energy prey close to the breeding season (Page et al., 2005a), and Australian fur seals make longer foraging trips (Arnould and Hindell, 2001), but neither increase their foraging effort (Kirkwood et al., 2006). Therefore, it is possible that to aid fat accumulation without an increase in foraging effort, fur seals depress their metabolism and, possibly, encounter more prey items as a result of an increase in prey availability.

Sea lions

Australian sea lions show little variation in metabolic rate throughout the year, as demonstrated by the lack of significance of month in the overall model. This is consistent with results of Williams et al. (2007), who found that the resting metabolic rate of Californian sea lions (*Zalophus californianus*) showed little change across seasons. Sustaining a consistent sSMR may be a strategy for sea lions to maintain their asynchronous breeding cycle. The lack of seasonal

variation in the metabolic rates of Australian sea lions is reflected in their temporally stable and geographically fixed foraging patterns (Lowther et al., 2011, 2013). Despite substantial individual variation in foraging strategies, Australian sea lions forage at the same trophic level in the same regions over seasons and years (Lowther et al., 2011, 2013). There were no seasonal changes in metabolic rates observed (present study) or foraging strategies (Lowther et al., 2011), and the availability of sea lion prey is consistent, even if low, year round (McIntosh et al., 2006; Peters et al., 2015). This means that Australian sea lions are likely to adopt other behaviour strategies, such as increasing their food intake, to cope with additional energetic costs throughout the year (e.g. lactation; Williams et al., 2007).

As male Australian sea lions are not able to use seasonal cues in their environment to predict the onset of the breeding cycle, we contend that they maintain a constant sSMR and a static foraging strategy, remaining close to the breeding colonies, in order to be prepared for breeding with females at any time of year (Lowther et al., 2013; Ahonen et al., 2016). This is likely to be an adaption to a low-productivity environment that is fairly constant (McKenzie et al., 2005; Villegas-Amtmann et al., 2009). The breeding period of Australian sea lions lasts for 120 days, suggesting that males must have an extended period of spermatogenesis (Ahonen et al., 2016). Males conserve energy by 'mate guarding', i.e. choosing a single female to mate with from when they haul out until they go into oestrus (Higgins, 1990). After mating, they leave to forage or to mate at another nearby colony, and therefore may not have the option of layering additional blubber before the next period when spermatogenesis and mate guarding occur (Ahonen et al., 2016).

Temperature

We show that some of the variation in metabolic rates of otariids can be explained by changes in natural fluctuations in water temperature within each facility (Figs 5 and 6). Although we did not measure the sSMR of otariids in water <16°C, there appears to be an increase of sSMR with increasing water temperature for fur seals (Fig. 5A–D) and a decrease in sSMR with increasing water temperature for sea lions (Fig. 6A–D). Sea lions that were housed at the highest latitude (RF3) did not demonstrate variations in sSMR from 22 to 26°C. The different responses to temperature are likely to result from differences in thermoregulatory strategies. Fur seals rely on a thick layer of fur to thermoregulate, because the blubber layer they maintain is metabolically inert and used primarily for energy storage (Liwanag et al., 2012a; Dalton et al., 2014a). Sea lions rely on a thicker blubber layer to protect themselves from cold water (Mellish et al., 2007; Williams et al., 2007; Liwanag et al., 2012b), which is interspersed with layers of muscle (Mellish et al., 2004). It is possible that the metabolic rate of sea lions declines during warmer temperatures as they use their metabolically active blubber layer through blood perfusion—dilating blood

vessels to allow blood to flow through and be warmed by the outside temperature (Meagher et al., 2008; Liwanag et al., 2009)—thus reducing the metabolic costs of maintaining a constant body temperature.

Maintenance of these thermoregulatory strategies is correspondingly different in the two families, each with its own energetic cost. Fur seals use a layer of air trapped between their fur layers to insulate their body. This allows the skin to be maintained at body temperature, but requires that fur seals spend a significant amount of time grooming their pelage (Battaile et al., 2015). This is an energetically expensive tactic (Liwanag, 2010), but could be complementary in cold water because it would raise metabolic rate. At warm temperatures, fur seals increase their metabolic rate in order to encourage blood flow to the flippers that are unprotected by hair to cool down (Dalton et al., 2014a), whereas in cool temperatures fur seals restrict blood flow to these areas in order to minimize heat loss (Mostman-Liwanag, 2008). As sea lions rely solely on their blubber to remain warm, they must retain a thicker layer than fur seals to compensate (Scholander et al., 1950), which can be maintained only by consuming large amounts of energy. Sea lion blubber thickness appears to remain constant throughout the year (Mellish et al., 2007), which may be why the metabolic rate of sea lions remains relatively constant across months but declines when water temperature increases. Despite the substantial differences in the thermoregulatory strategies of otariids, there was little difference in their overall sSMR, suggesting that these strategies have complementary costs.

Sex

A significant effect of sex on sSMR was found for both sea lions and fur seals, where females had higher sSMR than males. This same effect has been found in other species of adult pinniped, including Californian sea lions (Hurley and Costa, 2001), grey seals (Beck et al., 2003) and Antarctic fur seals (Arctocephalus gazella) (Boyd and Duck, 1991; Boyd and Croxall, 1996). Pinniped juveniles and pups do not show any significant sex differences in their metabolic rates, instead maintaining a consistently elevated metabolic rate associated with the cost of growth (Fowler et al., 2007; Verrier et al., 2011). As they age, morphological and physiological differences arise, including extreme sexual dimorphism and an elevated sSMR in the female (Hurley and Costa, 2001) that does not change depending on reproductive status (Williams et al., 2007). Females are usually in a stage of reproduction throughout the year (lactating or pregnant), whereas males spend some of the year removed from reproductive constraints. By measuring females that were non-breeding and non-lactating we removed the effect of reproduction, yet females still had elevated sSMR in comparison to the males. Therefore, the higher sSMR that we observed was probably related to the ongoing costs of reproduction. As there is no evidence that the metabolic rate of otariids varies between reproductive and non-reproductive cycles

Table 2: Mean ± SD and *n* of mass-specific standard metabolic rate (in millilitres of oxygen per minute per kilogram) and multiples of Kleiber's (1975) predicted basal metabolic rate (BMR*) for an Australian fur seal female and male, three New Zealand fur seal males, five Australian sea lion females and two Australian sea lion males measured in different months

Month	Measure	Feb	Mar	May	Jul	Aug	Sep	Oct	Nov	Dec
Australian fur seal										
AFF1	sSMR	7.0 ± 0.2	**6.1 ± 0.5**	NA	NA	6.3 ± 0.6	5.0	NA	6.7	8.2 ± 0.5
	BMR*	2.1	**1.8**			1.9	1.5		1.5	2.0
	n	3	**4**			2	1		1	2
AFM1	sSMR	**6.7 ± 0.5**	**5.5 ± 0.4**	NA	NA	3.6 ± 0.8	3.1	NA	4.9	6.1 ± 0.5
	BMR*	**2.6**	**2.1**			1.4	1.2		1.8	2.3
	n	**3**	**7**			2	1		1	2
New Zealand fur seal										
NFM1	sSMR	**6.5 ± 0.3**	**6.1 ± 0.2**	NA	NA	4.0 ± 0.3	NA	NA	5.4	4.3 ± 0.00
	BMR*	**2.3**	**2.0**			1.4			2.0	1.5
	n	**3**	**6**			3			1	2
NFM2	sSMR	NA	NA	5.8 ± 0.2	NA	NA	NA	NA	5.2 ± 0.1	NA
	BMR*			1.9					1.9	
	n			2					2	
NFM3	sSMR	**8.2 ± 0.02**	**9.8 ± 0.4**	8.8 ± 0.5	5.9 ± 0.2	6.7	NA	NA	7.5 ± 0.2	NA
	BMR*	**2.5**	**2.7**	2.4	1.7	1.9			2.1	
	n	**3**	**2**	2	2	1			2	
Australian sea lion										
ASF1	sSMR	8.1 ± 0.5	7.2 ± 0.4	9.2	9.7 ± 0.4	NA	NA	8.8	7.1	NA
	BMR*	2.2	1.9	2.4	2.6			2.4	1.9	
	n	3	3	1	3			1	1	
ASF2	sSMR	7.9 ± 0.4	7.8 ± 0.4	NA	NA	**7.0 ± 0.9**	7.6	NA	7.1	7.9 ± 0.1
	BMR*	2.2	2.2			**1.9**	2.1		2.0	2.3
	n	3	6			**2**	1		1	2
ASF3	sSMR	7.6 ± 0.6	6.3 ± 0.3			**7.0 ± 0.6**			7.2	7.6 ± 0.4
	BMR*	2.3	1.9	NA	NA	**2.1**	NA	NA		2.2
	n	3	6			**3**			1	2
ASF4	sSMR	6.7 ± 0.1	5.9 ± 0.3	**7.5 ± 0.8**	7.5 ± 0.3			6.4	5.7	
	BMR*	2.2	2.2	**2.0**	2.1	NA	NA	2.0	2.3	NA
	n	3	3	**2**	3			1	1	
ASF5	sSMR	9.3 ± 0.3	8.1 ± 0.3			**6.4 ± 0.9**			6.3	7.6 ± 0.2
	BMR*	2.8	2.4	NA	NA	**1.9**	NA	NA	1.9	2.3
	n	2	5			**3**			1	2
ASM1	sSMR	5.9 ± 0.3	5.6 ± 0.4	6.5 ± 0.2	7.5 ± 0.3			**8.2**	**7.2**	
	BMR*	2.1	1.9	2.2	2.5	NA	NA	**2.7**	**2.4**	NA
	n	3	2	2	3			**1**	**1**	

(Continued)

Table 2: continued

Month	Measure	Feb	Mar	May	Jul	Aug	Sep	Oct	Nov	Dec
ASM2	sSMR	**4.9 ± 0.3**	**4.2**	6.0 ± 0.2	6.0	5.8 ± 0.4			5.1 ± 0.6	
	BMR*	**1.8**	**1.6**	2.2	2.2	2.2	NA	NA	1.9	NA
	n	**5**	**1**	2	1	2			2	

Abbreviations: AFF, Australian fur seal female; AFM, Australian fur seal male; ASF, Australian sea lion female; ASM, Australian sea lion male; BMR, basal metabolic rate; NFM, New Zealand fur seal male; SMR, standard metabolic rate; sSMR, mass-specific standard metabolic rate. The number following the species and sex identity is an individual identifier. Bold values indicate months when the seal was moulting. NA indicates a month when that individual was not measured.

(Costa and Gentry, 1986; Williams *et al.*, 2007), these differences in sSMR are likely to be attributable to allometry (Kleiber, 1975; McNab, 2008).

Moult

In pinnipeds, the moult usually occurs following the breeding period, either immediately after breeding or following a brief foraging period (Scheffer and Johnson, 1963). For Australian and New Zealand fur seals the moult occurs early in the year for ~2 months. Australian sea lions can moult at any time of year, and the moult is generally extended over 3–5 months. Metabolic responses to this phenomenon differ across species, and the energetic processes behind the moult are not well understood. In our study, the male fur seals increased sSMR during the moult, but there was no consistent effect of moult on the sSMR for any of the other otariids. Harbour, spotted (*Phoca largha*) and northern elephant seals (*Mirounga angustirostris*) have low resting metabolic rates during their moult (Ashwell-Erickson *et al.*, 1986; Worthy *et al.*, 1992). The metabolic rate of northern fur seals (*Callorhinus ursinus*) was highest during autumn and lowest in the winter, which corresponded to the beginning and the end of the moult (Dalton *et al.*, 2015). Grey seals and non-reproductive Californian sea lion females showed increased metabolic rate during the moult; juveniles significantly more than adults (Boily, 1996; Boily and Lavigne, 1997; Beck *et al.*, 2003; Williams *et al.*, 2007). Increasing metabolic rate during the moult is proposed to aid in thermoregulation for fur seals while some of the insulating layer is lost and the energy invested into the growth of new hair (Boyd *et al.*, 1993). Decreasing metabolic rate is proposed to delay fat loss while hauled out during the moult (Beck *et al.*, 2003).

As sea lions do not rely on their fur layer for thermoregulation, their energetic response to the moult is likely to differ from that of the fur seals. During the moult, the blubber layer and lipid content of Californian sea lions is at its lowest, suggesting that an increase in metabolism is required to maintain body temperature within the thermoregulatory range (Williams *et al.*, 2007). As the sea lions in our study were housed in warm water for the duration of their moult, the effect of the moult may have been masked. The female sea lions displayed no discernible pattern in sSMR during the moult (Table 2). The two male sea lions in this study moulted at different times of the year, one during the warmest water period (25–26°C), when we recorded his highest sSMR (ASM1; Table 2), and the other during moderate water temperatures (19–20°C), when we recorded his lowest sSMR (ASM2). If the sea lions do indeed use perfusion to cool during warm temperatures, this effect may have been exacerbated by the moult, allowing the body to cool more quickly and slowing their metabolism. During the period of moderate water temperatures, the sea lions may need to increase their metabolic rate to cope with the cooler water and hair loss. Seal moult generally occurs in summer to maximize skin surface temperature for the promotion of hair growth (Paterson *et al.*, 2012) and because they are unable to thermoregulate efficiently (Feltz and Fay, 1966).

Implications for a changing environment

Australian sea lions typically forage in temperatures of 12–22°C in South Australia (Lowther *et al.*, 2013). Male New Zealand fur seals forage in waters around Macquarie Island (54°S, 159°E), where the water temperature can be as low as 2°C, to Montague Island (36°S, 150°E) and across to western Australia (33°S, 114°E), where the water can reach 24°C (Campbell *et al.*, 2014; McIntosh *et al.*, 2014). Australian fur seals are found predominantly in the Bass Strait, southern Australia, where water temperatures have a much smaller range of 12.6–19.3°C (Kirkwood *et al.*, 2006; McIntosh *et al.*, 2014). Therefore, the fur seals and sea lions in our study were exposed to a range of temperatures that were at the upper limit of what they would experience in the wild. Despite prolonged exposure to water temperatures higher than those that seals would experience in the wild, metabolic rates were not outside those expected for a marine mammal (Williams *et al.*, 2000). It is possible, therefore, that the fur seals and sea lions housed in captivity have acclimated to warm water. South-east Australia is expected to have some of the largest increase in sea surface temperature globally with 0.7–1.4°C warming by 2030 (Ridgway and Hill, 2012; Carroll *et al.*, 2016), and the present study presents evidence that the fur seals and sea lions that occupy this area have the physiological capacity to adapt to these changes.

Conclusions

Pinnipeds that have a limited ability to adjust their energy storage and usage may be more susceptible to environmental change. Maximizing fitness can, in part, be achieved through

adjusting metabolic rates in response to changes in environmental conditions. Flexibility in physiological and morphological traits is important to survival, because mammals that have static metabolic rates and core body temperatures are more likely to become extinct (Geiser and Turbill, 2009). Australian fur seals and New Zealand fur seals demonstrated annual variations in their standard metabolic rates, which corresponded to their annual breeding and moulting cycle. Australian sea lions showed very little variation in metabolic rate over the year or in response to the moult, but metabolic rate reduced in response to increasing water temperatures. Otariids in the present study have demonstrated adaptations to warming water, a trait that might enhance their survival in a changing environment. Fur seal numbers in Australia are increasing, whereas sea lions are in decline and classified as endangered. Sea lions may compensate for living in a low-productivity environment by using an 18 month breeding cycle and a static foraging strategy and energy usage (Lowther and Goldsworthy, 2011; Ahonen *et al.*, 2016). It is unclear at this stage whether the sea lion strategy means that they are ready to withstand further change, or they may not persist under more extreme pressures. In contrast, fur seals may be buffered by their potential to use their pelagic diving abilities to move offshore and exploit cold upwellings.

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