Mass-dependent energetics and survival in Harbour Seal pups

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Summary

1. Winter survival rate in Harbour Seal pups is significantly correlated with the autumn body mass of pups. Multi-type mark–recapture statistics were applied to individual re-sighting histories of branded seals, and survival probability was estimated with weight as a covariate. The probability of surviving to an age of 1 year is only 0·63 for the smallest pups at 17 kg, whereas pups at 32 kg have a survival probability of 0·96.

2. An energetic model for juvenile Harbour Seals reveals how metabolic rate is related to body mass, skin surface area, blubber thickness and water temperature. There is an increasing thermal stress with decreasing body size of pups. Low winter water temperatures induce a negative energy balance in small pups, which is a probable cause of the observed mass-dependent survival.

3. This study explicitly links a physical property of the environment, sea-water temperature, to energetics and life history. The approach opens possibilities for studying aspects of life-history evolution, such as optimal weaning weight and pupping time, in marine mammals.

Key-words: Cold stress, life-history evolution, marine mammals, seasonality, thermoregulation

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Introduction

Understanding how environmental conditions influence the life history of a species is fundamental for the analysis of population dynamics and evolution. Fluctuations in the environment constrain which life-history strategies are successful (Costa & Gales 2003). The predictability of the environment influences for example the optimal size of offspring and the timing of reproduction (Tuljapurkar 1990; Houston & McNamara 1999). In most mammals, including pinnipeds, yearlings are the most sensitive to environmental conditions and, consequently, first year survival is the most variable of the demographic parameters (Wickens & York 1997). There are several external factors that can influence first year survival. Pups of the year are often more vulnerable to predators (Boveng *et al.* 1998; Lucas & Stobo 2000), parasites (Breuer *et al.* 1988) and changes in food supply (Stewart & Lavigne 1984; Trillmich *et al.* 1986; Lunn, Boyd & Croxall 1994; Kjellqwist, Haug & Øritsland 1995; Trillmich *et al.* 1991). The variation in survival rates also depends on the body condition of individual pups (Boltnev, York & Antonelis 1998). The weight at weaning is significantly correlated with first year survival in for example: Southern Elephant Seals (*Mirounga leonina*) (McMahon, Burton & Bester 2000), Northern Fur Seals (*Callorhinus ursinus*) (Baker & Fowler 1992) and Grey Seals (*Halichoerus grypus*) (Hall, McConnell & Barker 2001).

The mechanisms leading to lower survival rates of pups in poorer than average condition at weaning are complex, but impeded feeding success owing to limited diving capacity and lower swimming speed can be important (Burns 1999; Horning & Trillmich 1999; Bowen *et al.* 2001). Just as in terrestrial mammals, constrained energy budgets can lead to nutritional deficiency and starvation (Trillmich *et al.* 1986; Clutton-Brock, Albon & Guinness 1994; Stewart 1997). One entry in the energy budget of mammals is the cost for thermoregulation. In terrestrial mammals the heat production resulting from normal metabolism and dense fur can often suffice for keeping a constant body temperature even in low air temperatures (Scholander *et al.* 1950). The situation can be dramatically different for aquatic mammals since the conductivity of water is 23 times that of air (Irving & Hart 1957; Hart & Irving 1959; Donohue *et al.* 2000).

Harbour Seals (*Phoca vitulina*) are distributed over latitudes where water temperatures show pronounced seasonal changes. Pups are born in early summer and

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Table 1. Numbers of pups of Harbour Seals that were caught in the Koster area in the northern Skagerrak in autumn over the period 1984–93

Sex	1984–1986	1989–1991	1992–1993	Total
Male	16	16	27	59
Female	25	28	21	74
Total	41	44	48	133

weaned a month later. Different weaning weights and individual variation in foraging success after weaning during a few critical summer months lead to a range of body sizes in pups as the cold period approaches. In this study, we investigate size-dependent survival probability of 4-month-old Harbour Seal pups. We elaborate an energetic model, estimating the energy requirements for pups of different sizes in relation to the seasonal flux in water temperature. Our approach provides a tool to examine selection imposed by different sea-water temperatures on body size in Harbour Seals.

Materials and methods

Harbour Seal pups were captured in the northern part of the Skagerrak on the Swedish west coast over the period 1984–93 (Table 1). Weights and lengths of 133 pups were measured and permanent freeze brands were applied. Handling of seals was carried out according to permits given by the Ethical Board of the County Court in Göteborg, Sweden. Freeze branding does not cause open wounds and the affected skin surface area is less than 1% of the total body area. The seals were captured only once (at the branding occasion) and subsequently observed at their natural haul-out sites with telescopes from a distance. Branded seals have not shown any signs of increased mortality after their release (Härkönen, Harding & Lunneryd 1999), the branding method is thoroughly described in Härkönen *et al.* (1999).

During subsequent years (1985–2002) the animals were studied in a systematic programme examining age- and sex-specific haul-out behaviour (Härkönen *et al.* 1999; Härkönen & Harding 2001). Included in the present study are a total of 3371 re-sightings collected during 590 observation days. Pup weights and capture dates are presented in Fig. 1. Since the age at capture varied somewhat, we tested whether age influenced the result. We undertook the full statistical analysis both with the original weights at capture and with adjusted weights. Adjusted weight was defined as the expected weight of pups at a given reference date (1 October), assuming they would follow the mean rate of increase in body weight (Fig. 2). Both non-adjusted and adjusted weights gave the same result (and thus age at capture did not distort the analysis). Therefore we use the adjusted weights (Fig. 2).
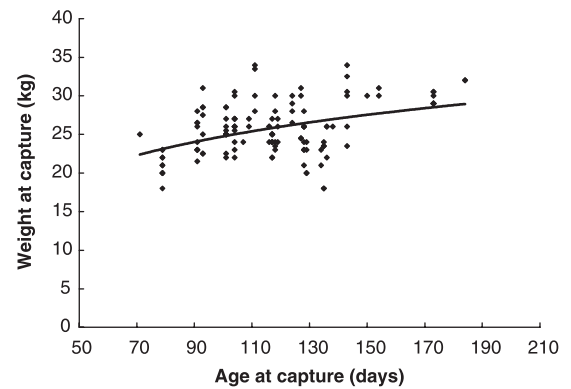
Fig. 1. Weight and age at capture of Harbour Seal pups. The equation for the fitted line is $y = 6{\cdot}89 \ln(x) - 6{\cdot}98$, $R^2 = 0{\cdot}17$, $N = 133$.
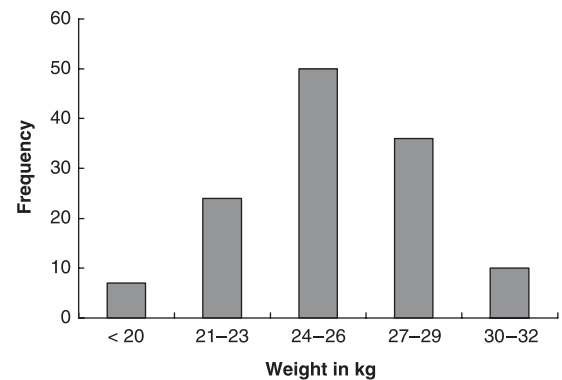
Fig. 2. Histogram of estimated Harbour Seal pup weights at a reference day (1 October). The original capture weights shown in Fig. 1 were compensated by the expected mean growth during the time period (function given in Fig. 1). These compensated weights are considered more appropriate for comparisons of weight-dependent survival. However both adjusted and unadjusted weights gave the same result in the analysis of weight-dependent survival. $N = 133$.

SURVIVAL PROBABILITY

The branding and re-sighting data were treated as mark–recapture data, and a standard method was applied to estimate survival probability (Lebreton *et al.* 1992; Nichols *et al.* 1992; Fujiwara & Caswell 2002). All calculations were done in MATLAB (MATLAB 2001) using the algorithm presented in Fujiwara & Caswell (2002). Previously, this method was successfully applied to analyse individual sighting histories of the North Atlantic right whale (*Eubalaena glacialis*) (Fujiwara & Caswell 2001).

The stage-specific survival probability $(s_i^{(j)})$ is the probability that individual j in stage i will survive to the following year. We categorized the individuals based on ages as follows: (1) pups, (2) ages 1 and 2, (3) ages 3 and 4, and (4) ages 5 and older, and assigned stages 1, 2, 3 and 4, respectively. Individuals were considered 'marked' when they were branded, and considered 'recaptured' in subsequent years if they were re-sighted at least once in a year. We expect heterogeneity in

capture and survival probabilities among stages to be greater than among different years. Thus, all stage-specific capture probabilities and survival probabilities, except survival of stage 1 (pups), were assumed to be constant over time but to differ among stages.

We hypothesized that survival probability of pups was related to their weight in October when they were caught. To test this hypothesis, we modelled the survival probability of individuals as a logistic function of their weight:

$$s_1^{(j)} = \frac{\exp(\alpha + \beta w_j)}{1 + \exp(\alpha + \beta w_j)} \quad \text{(eqn 1)}$$

where α and β are intercept and slope parameters and w_j is the mass of individual j. Then our null hypothesis is $\beta = 0$, and the alternative hypothesis is $\beta \neq 0$. This hypothesis was tested using a likelihood ratio test (Lebreton *et al.* 1992).

ENERGETICS

The energy balance for thermoregulation (E) is heat production (P) minus heat loss to the environment (H) and is a function of body mass (w) and water temperature (t)

$$E(w,t) = \begin{cases} P(w) - H(w,t) & \text{if } H(w,t) > P(w) \\ 0 & \text{if } H(w,t) \leq P(w) \end{cases}$$
$$\text{(eqn 2a, b)}$$

If the heat loss exceeds the energy production (equation 2a) the animals must increase their metabolism by the same amount to maintain their core body temperature (Irving & Hart 1957; Øritsland & Markussen 1990). We assumed the energy balance to be zero if the animal is not cold stressed (equation 2b), since overheating is not a problem at our latitudes (see Noren 2002 for a study of the opposite case). Heat production (P) was assumed to be equal to the field metabolic rate (FMR) (e.g. Lavigne 1982). The FMR is the average heat production by a free-ranging animal and includes a normal blend of activities over a day. For seals it involves resting, calm swimming, migratory swimming and feeding (Ørtisland & Markussen 1990). The relationship between FMR and weight was estimated according to Boyd (2002) as FMR = $30 \cdot 43 w^{0 \cdot 524}$, where the FMR is given in watts (W). We estimated the heat loss (H) by a general function, modified from Worthy (1991) and Kvadsheim *et al.* (1997) as:

$$H(w,t) = \frac{c * A(w) * (T - t_s)}{d(w)} \quad \text{(eqn 3)}$$

where c is the thermal conductivity of blubber at $0 \cdot 19$ W m^{-1} K^{-1} (Kvadsheim & Folkow 1997), $\Delta T = T - t_s$ is the difference between the body core (T) and the ambient water temperature t_s (Øritsland & Markussen 1990). The body temperature of Harbour Seals is
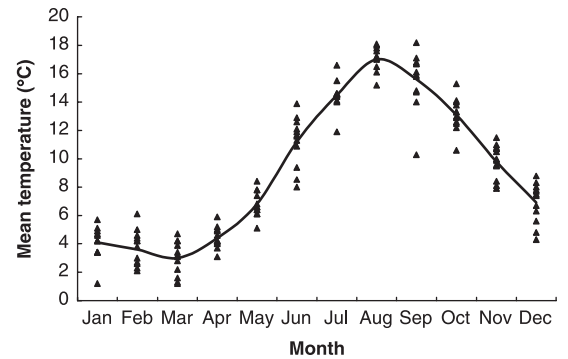
Fig. 3. Seasonal flux in water temperatures at the study site (northern Skagerrak, Sweden). Each black triangle represents the monthly mean temperature in a single year and is an average of measurements at 0–30 m depths. The measurements were repeated during 12 years and the curve indicates the mean temperature for all years. Data from the Swedish meteorological and hydrological institute (SMHI).

about 37 °C (Hind & Gurney 1998). $A(w)$ is the body surface area (m^2) and $d(w)$ is the blubber thickness in metres. There is a general tendency for blubber thickness to increase with body mass in pinnipeds (Ryg *et al.* 1993). Although blubber thickness in adult seals varies over the year, juveniles have a more uniform blubber thickness (Rosen & Renouf 1997). Mean blubber thickness of Harbour Seals was obtained from a curve fit of morphometric data: $d(w) = (10 \cdot 23 \ln(w) - 10 \cdot 74)/1000$, where d is given in metres. The body surface area of a seal was estimated using Meeh's equation: $A(w) = kw^{0 \cdot 67}$ (Lavigne 1982), where A is the total surface area (m^2) and w is the body mass (kg). We used Meeh's constant: $k = 0 \cdot 08$ (Irving *et al.* 1935; Lavigne 1982).

Water temperature (t_s) data were provided by the Swedish meteorological and hydrological institute (SMHI). We used monthly mean water temperatures at depths 0, 2, 5, 10, 15, 20 and 30 m (Fig. 3). This represents well the water temperature at the depths where the seals dive in the study area (Härkönen 1987).

Results

Multi-type mark–recapture statistics were applied to individual capture histories of Harbour Seals, accounting for differences in capture and survival probabilities among age-specific life stages. In addition, we accounted for weight-specific differences in survival probability of pups by modelling the probability with actual weight as a covariate. Our analysis shows that winter survival probability of Harbour Seal pups was an increasing function of their autumn body weight. A pup with 17 kg autumn body weight only had a 0·63 chance of survival, while a large pup at 32 kg had a 0·96 chance to survive to the age of 1 (Fig. 4). The slope of the survival probability curve (β in eqn 1) is significant ($P = 0 \cdot 044$), supporting our hypothesis that weight and survival probability of pups are positively correlated.
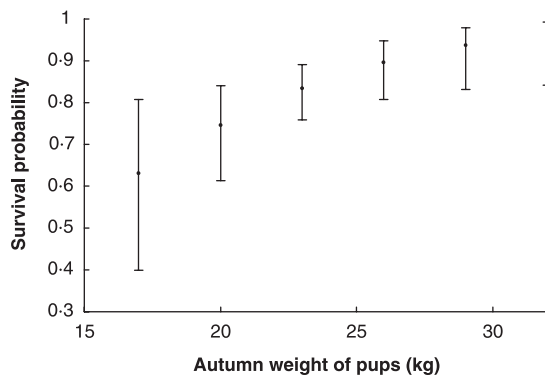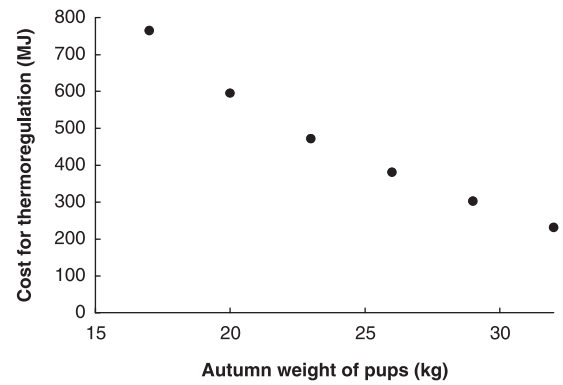
Fig. 4. First year winter survival of Harbour Seal pups in the northern Skagerrak is significantly related to their body mass in the autumn. Error bars denote 95% confidence limits for each given weight.
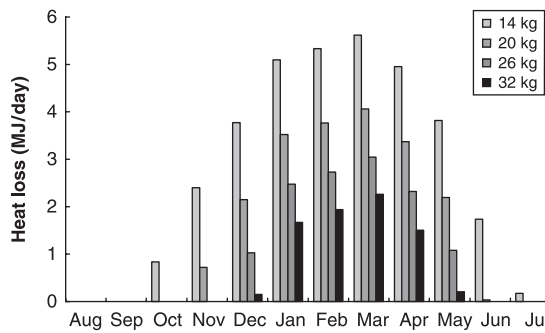
Fig. 5. Seasonal variation in energy expenditure by thermoregulation in pups of different sizes.

Fig. 6. Total heat loss over the winter declines with increasing pup size.

There is a substantial seasonal variation in heat loss linked to body weight (Fig. 5). The heat loss is lower than the metabolic heat production during the summer and early autumn, but considerably greater in other seasons, when all size classes of pups must increase their metabolic rates to maintain body temperature. However, small pups are low-temperature stressed for a longer time of the year than heavy pups (Fig. 5). A 20-kg seal starts to get cold stressed in November (at a water temperature of 9·8 °C), a 26-kg seal in December (at 6·9 °C) and a 32-kg seal has a close to neutral energy budget until the beginning of January when water temperature falls to 4·1 °C. It is also evident that small pups must spend more energy on thermoregulation per day over the entire cold period. In the coldest month, March, a 17-kg seal has to spend 4·74 MJ day^{-1} to compensate for heat loss whereas a 32-kg seal spends at most 2·26 MJ day^{-1}. Converted into food intake this represents an extra 0·9–1·0 kg of fish per day (Härkönen & Heide-Jørgensen 1991) for the 17-kg pup. The 32-kg seal would need to ingest only 0·4–0·5 kg fish extra per day during the coldest month to compensate for heat loss.

We estimated the total energy required to compensate for heat loss over the winter (October to June) for pups in size range 17–32 kg and found that the smallest pups would need 765 MJ, whereas the heaviest would require 232 MJ extra for thermoregulation (Fig. 6). Both heat loss and survival are functions of weight. Hypothesizing that there is a functional response between mean survival rate and the total heat loss (Figs 4 and 6) gives a close to linear function where, above 230 MJ, each additional 100 MJ lost to thermoregulation represents a 6% decrease in survival probability.

Discussion

We show that small Harbour Seal pups at 4 months of age have substantially lower chances of surviving winter compared with their heavier peers. It seems important to reach at least 26 kg in the autumn, since the survival rate declines steeply for smaller seals (Fig. 4). Investigating the seasonal variation in water temperature, and elaborating an energetic model for Harbour Seals, we found that the cost of thermoregulation varies dramatically with body size (Figs 5 and 6). The finding that small Harbour Seals can be cold stressed within their natural range of water temperatures is supported by an experimental study by Irving & Hart (1957). They found that the smallest Harbour Seal, 19·4 kg, significantly elevated its metabolism as water temperature decreased from 20 °C to 0 °C. The other four seals in the study (26·8–41·0 kg body weight) increased their metabolism only slightly at lower temperatures.

The heat loss must be compensated for by increased food intake or protein and fat catabolism since seals maintain a constant inner body temperature (Irving & Hart 1957; Worthy 1991). Increasing food intake requires a different daily time budget, where time used for diving would increase, and the time for resting would decrease. Obviously, there must be an upper limit to the amount of food that can be caught and metabolized during a day. If the energetic demands cannot be met by ingestion, seals utilize protein and fat tissue and lower their metabolic rate to a starvation mode (Øritsland & Markussen 1990, Noren & Mangel 2004). Fat catabolism is a short-term solution in cold seasons since it leads to even higher heat loss owing to decreased insulation. We suggest that the observed

pattern of declining survival rates in small seal pups is strongly related to cold stress.

The mass-dependent winter survival of pups poses an additional challenge to adult female seals. In order to optimize their fitness they should adjust the timing of pupping to the seasonal flux in sea-water temperature to minimize heat loss for their pups. Harbour Seal pups average 8·7 kg (95% CI: 7·9–9·5 kg) at birth (Härkönen & Heide-Jørgensen 1990). Harbour Seal populations exhibit a geographical cline in pupping season, where the mean date for pupping is about 4·1 days later per latitudinal degree north (Temte, Bigg & Wiig 1991; Temte 1994). It seems likely that mean water temperature in the spring is critical for pupping time. However, the timing of the pupping season should not only minimize heat loss in newborns, but also, as the present study indicates, be adjusted to give pups time to grow to a size in the autumn that minimizes winter mortality.

Harbour Seal females make a substantial energetic transfer to their pups, losing up to 40% of their body weight during the 30-day lactation period (Härkönen & Heide-Jørgensen 1990; Muelbert & Bowen 1993; Bowen *et al*. 1994). During lactation pups gain 0·4–0·55 kg per day (Dube, Hammill & Barrette 2003; Muelbert, Bowen & Iverson 2003), and are weaned at about 20 kg (Härkönen & Heide-Jørgensen 1990; Bowen *et al*. 1994; Grahl-Nielsen *et al*. 2000). Harbour Seal pups then undergo a postweaning fast for 5 weeks, losing about 20% of their weaning weight before they can start to feed more efficiently (Muelbert & Bowen 1993; Hansen, Lavigne & Innes 1995). These 2-month-old pups at about 15 kg can now only forage for a few months before the onset of winter. Mean weight of 4-month-old pups in our study area was 24 kg (Härkönen & Heide-Jørgensen 1990; current study). If pups had continued to fast they would theoretically weigh about 8 kg in October. Consequently, the weight of pups 4 months after birth is a combination of the weaning weight and the energy ingestion after the postweaning fast. This means that Harbour Seal pups are sensitive to food availability and that annual fluctuations in food supply can affect survival of entire cohorts. We also expect female body size and pup body size at weaning to be larger in colder waters with short summers. Such predictions of optimal strategies can be investigated using state-dependent dynamic models (Houston & McNamara 1999; Noren & Mangel 2004).

THE ENERGETIC MODEL

Heat loss to the environment has often been treated as part of the field metabolic rate and averaged over age classes in energetic models (e.g. Winship, Trites & Rosen 2002). We have here instead chosen an approach to estimate FMR and heat loss that allows mass-dependent heat loss to be assessed for any given temperature. A model including adults would require sub-models for moult, lactation, breeding, etc. Energetics of adults also require specific modelling of the blubber layer, since it varies substantially over the body surface, and over the season (Beck & Smith 1995; Rosen & Renouf 1997). The present model could be kept simple since we were concerned with the energetics of pups of the year only.

Heat flow in seals is not a trivial issue and has been the subject of many ambitious but not always unanimous studies. The discussions concern, for example, the area and shape of a seal, the functional blubber thickness and the nature of heat convection over fur in turbulent water (e.g. Kvadsheim *et al*. 1997; Boily, Kvadsheim & Folkow 2000). Although the more complex models include several important features, they have not been more successful in predicting experimental results, and simple models based on blubber conductivity have been recommended (Ryg *et al*. 1993; Watts, Hansen & Lavigne 1993; Boily *et al*. 2000). However, even with simple heat models there are many model assumptions to consider. We have used the maximum insulating capacity of blubber, which minimizes heat loss estimates. If we had assumed some circulation of blood in the fat layer this would increase the estimated heat loss. On the other hand, we calculated the temperature difference across the blubber only. Some studies have argued that the temperature gradient in the tissue below the blubber acts as a shield, slowing down cooling (Worthy 1991). However, a counter argument would be that warming up this cool blood before it enters the heart will require extra heat production. Furthermore, we might underestimate heat loss by assuming that the whole body has the same high insulation capacity, whereas the head and tail regions are known to have higher heat loss (Kvadsheim & Folkow 1997). On the other hand, we included flippers in the surface area, which tends to exaggerate heat loss. Some studies exclude all flippers or only front flippers from the surface area of a seal (Watts *et al*. 1993).

In estimating heat loss we assumed that the seals spend all their time in water. This is appropriate for the present study since we only investigated energetics in pups under winter temperatures. Pups haul out less than 20% of their time in the winter, and spend about 86% of their time submerged when at sea (Bekkby & Bjørge 2000; Jørgensen *et al*. 2001). Hauling out in air is costly in winter owing to wind chill in cold air (and rain and snow) (Hind & Gurney 1998). Evaporation of water from the wet fur is very demanding energetically and takes heat from the seal body at about 2·5 MJ per kg water (Mauk *et al*. 2003). Thus, including a separate term for the heat loss in air would only marginally affect the estimated heat loss of the current study. In the summer, however, hauling out can be thermodynamically important for lean and small seals and certainly for newborn pups (Irving & Hart 1957; Hart & Irving 1959). Air temperature was found to be a critical factor determining pupping time of Northern Fur Seals (Trites & Antonelis 1994).

The present model could be fine-tuned to study different haul out behaviours over the full year. It could also take protein and fat content and metabolization into account separately. Although improvements are important, and might be pursued when the question in focus so demands, we believe that increasing the level of complexity would not increase our understanding of the current problem. The simple model we have developed here captures the main components of thermoregulation in Harbour Seal pups over the winter, and although modifications can alter each parameter value, the relative differences in energy budgets among animals of different sizes should remain.

Acknowledgements

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