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The impact of lactation strategy on physiological development of juvenile marine mammals: implications for the transition to independent foraging

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Abstract. Lactating marine mammals provision their offspring either by providing large amounts of lipid-rich milk over a short period during which females fast (capital provisioning), or smaller amounts of less energetically dense milk over an extended period during which females forage (income provisioning). While it has long been recognized that these two strategies carry different costs for the female, the effect of these two strategies on the physiological status of newly weaned pups has rarely been considered. Recent comparative studies on the development of diving capacity, as assessed by measuring total body oxygen stores, have demonstrated that the provisioning strategy does affect pup development. Phocid pups, which grow rapidly during their brief nursing period undergo a strong post-parturition anemia and are weaned with relatively immature oxygen stores, possibly due to limited iron intake. Otariid pups, which grow at a slower pace over a longer period, are weaned with body oxygen stores that are significantly more mature. This suggests that newly independent phocid pups must quickly develop foraging skills in order to acquire the nutrients necessary to mature physiologically. In contrast, newly weaned otariids have more mature oxygen stores, and may have previous foraging experience, which may allow for increased behavioral flexibility. © 2004 Elsevier B.V. All rights reserved.

Keywords: Lactation strategy; Harbour seal (*Phoca vitulina*); Steller sea lion (*Eumetopias jubatus*); Diving physiology; Development

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1. Introduction

Within the pinniped lineage, there are two main strategies used by females to provision their dependent offspring. Females either utilize a capital investment strategy, whereby most, if not all of the energy provided to the pup comes from the female's endogenous reserves, or an income-based strategy, whereby females provision their offspring initially from endogenous reserves that are later supplemented by periodic foraging trips [1]. All Otariidae and Odobenidae demonstrate the income provisioning strategy, while most Phocidae utilize the capital provisioning strategy [2,3]. Due to their small size, some phocids such as harbour and ringed seals, cannot store enough energy to provision their offspring without supplemental foraging [4]. That the maternal strategy used has a large impact on the growth and condition of the pups is clear. Phocid pups are provisioned with energy-rich milk, and as a result grow quickly and accumulate large lipid reserves during the short lactation period [5]. In contrast, otariid pups are suckled on less energetically dense milk, grow more slowly, and rarely show the large variation in body composition seen in phocid pups [2,6,7]. In addition to impacting growth rates, the lactation strategy may also impact physiological development during the dependent period. While physiological development takes many forms, for the purpose of this paper, we will focus on the development of body oxygen stores, as these are critical for sustaining diving and foraging activity in newly weaned and independent pups [8,9]. In addition, there is growing evidence that juvenile diving activities can be limited due to their smaller size and reduced mass-specific oxygen stores, as compared to adults [10–13]. Therefore, if the developmental patterns of capital and income provisioned pups differ, this may also affect how they interact with their environment in the weeks and months postweaning.

To determine if lactation strategy influences the pattern of physiological development, we compare the ontogeny of body oxygen stores in a phocid, the harbour seal (*Phoca vitulina*), and an otariid, the Steller sea lion (*Eumetopias jubatus*). Following a review of our work on age-related changes in haematology and body oxygen stores, we then present preliminary data on the iron status of juvenile and adult harbour seals. Limitations in iron intake have been implicated in developmental anaemia in terrestrial species that subsist on iron-poor milks [14,15]. Since heme levels strongly influence body oxygen stores, iron kinetics may also influence pinniped development [16,17]. We recognize that female harbour seals forage during the lactation period [4], and that this reduces the strength of our comparisons. However, because harbour seal pups demonstrate the rapid growth, large accumulations of lipid, and a short dependent period characteristic of most capital provisioned pups, we believe that the presented comparisons are valid.

2. Methods

2.1. Animal handling and oxygen store development

Data for harbour seals comes from work conducted in Monterey Bay, California from September 1997 through June 2000 (n=109) and Prince William Sound, Alaska in June 1998 and 1999 (n=113) [18], and 167 animals captured in Mont Joli, Quebec, Canada in the summers of 2000–2002 [16]. Steller sea lions (n=365) were captured throughout

Alaska in collaboration with Alaska Department of Fish and Game and the National Marine Mammal Laboratory [17]. At capture, all seals were weighed, sexed, and aged, and a subset of harbour seals handled in California (n=63) and Alaska (n=58) had their body composition determined by deuterium dilution [19]. To determine total body oxygen stores, an initial blood sample was collected from which haematocrit (HCT) and haemoglobin (Hb) were determined. Plasma volume was measured using the Evan's blue dye method [20], and blood volume (BV) was determined by dividing plasma volume by the measured HCT. Both blood and plasma volumes are reported on both an absolute and lean body mass-specific basis as available. Blood oxygen stores were determined following [21], using the individually measured HCT, Hb, and plasma volume. Muscle myoglobin content was determined from biopsy samples (<0.2 g) [22]. Total body oxygen stores were determined by adding the stores in lung, muscle and blood [21]. Further details on the capture and handling techniques, the methods used to measure body oxygen stores, and the statistical results are reported in the original publications from which this review is drawn [16–18].

2.2. Iron analyses

Iron status was determined for 73 harbour seals captured in Canada. Serum iron levels and total iron binding capacity (TIBC) were determined coulometrically using an ESA ferrochem II iron analyser [23]. Percent saturation was calculated as serum iron/TIBC. Serum ferritin concentration was measured by ELISA [24]. All iron assays were carried out at the Kansas State University College of Veterinary Medicine. General linear models were used to test for the effect of age and sex, and significant differences (p<0.05) identified by Bonferroni post hoc comparisons. To determine if iron status had a significant impact on blood oxygen stores, iron values were added as covariates to GLM models of age effects on oxygen stores. Prior to all analyses data normality was assessed using probability plots, and data transformed as necessary.

3. Results

3.1. Animal handling and oxygen store development

As expected, the growth rates and age-related changes in body composition differed between the two species. Harbour seals grew rapidly (0.56±0.01 kg day^{-1}) over the ~25-day lactation period and body condition increased from 10% at birth to 39.4±0.1% at weaning, before falling to an average value of 25.1±1.3% in yearling and adults [18,25,26]. In contrast, Steller sea lions grew at a slower rate (as determined from average mass values for each age class) of 0.3 kg day^{-1} between 1 and 9 months of age, and 0.12 kg day^{-1} between 9 and 21 months of age [17].

As results from the development of oxygen stores in each of these groups have previously been presented [16–18], data are only summarized here. Typically, neonates had elevated HCT and Hb values, which declined in the first days (harbour seals) to weeks (Steller sea lions) of life, then increased later in the nursing period (Fig. 1). For harbour seals, this drop in HCT and Hb caused a decline in mass-specific blood oxygen stores during the lactation period, as all age classes except the relatively hydrated neonates had similar plasma volumes [16,18]. The decline in mass-specific blood oxygen stores could

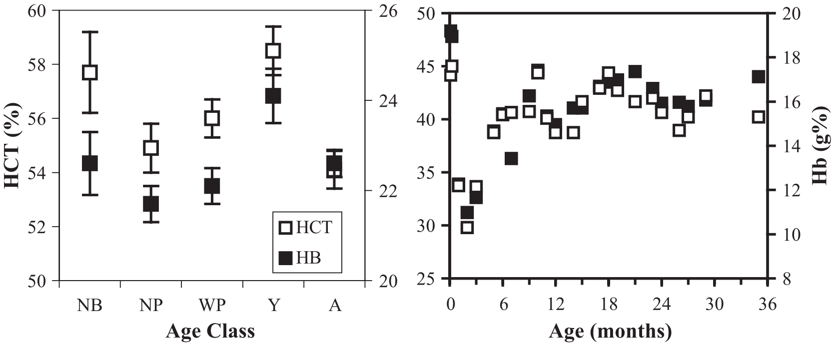

Fig. 1. Age-related changes in mean haematocrit (HCT) and haemoglobin (Hb) content in harbour seals from California [18], and Steller sea lions from Alaska ([17]; neonatal values from [28]). Harbour seal age categories are newborn (NB), nursing pup (NP), weaned (WP), yearling (Y), and adult (A).

not be attributed solely to age-related changes in body condition, as it persisted when stores were scaled to lean body mass [18]. Nor was there any effect of body composition on blood oxygen stores within any age class. In contrast, while Steller sea lions also showed elevated HCT, Hb, and plasma volumes in neonates [27,28], there was a gradual decline in mass-specific plasma volume over the first 21 months of life [17]. However, because HCT and Hb increased rapidly from 1 to 10 months (Fig. 1), blood oxygen stores were similar to those of adults by the end of the first year of life [17].

In harbour seals, muscle myoglobin concentration did not increase until after weaning, but reached adult values by the end of the first year of life [18]. There was no effect of body condition on muscle myoglobin concentration in any age class [18]. In contrast, average myoglobin levels increased gradually with age in nursing Steller sea lions, but did not reach adult levels until after the end of the second year [17].

Total body oxygen stores integrate all measured stores, and therefore also varied with age (Fig. 2). In harbour seals, total body oxygen stores declined with age from neonates through to weaning, and then increased in yearlings and adults, when measured on a mass-specific basis [16,18]. However, stores increased from birth to adulthood when measured

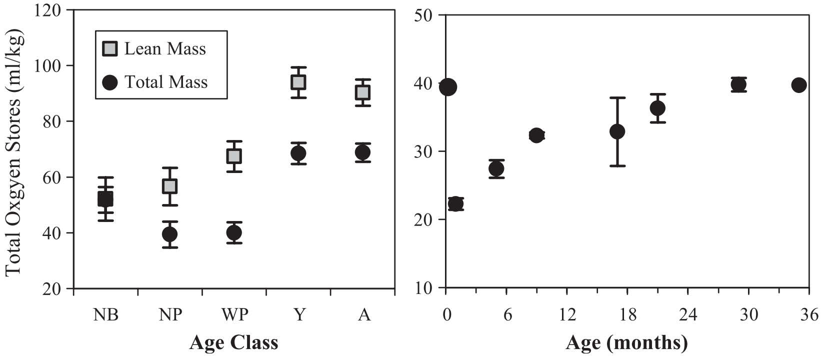

Fig. 2. Mean (±S.E.) total body oxygen stores for harbour seals, scaled to total and lean body mass [18], and Steller sea lions [14]. Neonatal Steller sea lion values taken from Ref. [27]. Age categories as in Fig. 1.

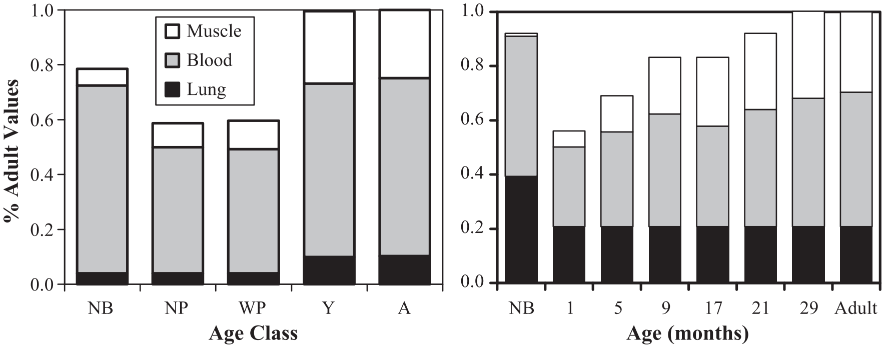

Fig. 3. Total body oxygen stores, as a percent of adult values, for harbour seals and Steller sea lions. Total stores are subdivided to show the relative contribution of lung, blood, and muscle oxygen stores. Age categories as in Fig. 1.

on a lean-body-mass basis [18]. In contrast, Steller sea lion total oxygen stores declined during the first month of life, but increased consistently after that, and reached adult values by the time juveniles were 21 months of age [17]. In both cases, the initial decline in oxygen stores was due to the early drop in HCT and Hb.

When the relative maturity of oxygen stores at different stages was compared between Steller sea lions and harbour seals, it was clear that while both species showed an initial decline in oxygen stores, harbour seals were not able to recover during the short nursing period, and so were weaned with oxygen stores that were small (52–60%) relative to those of adults [16,18]. In contrast, mass-specific oxygen stores increased during the lactation period in Steller sea lions, such that pups were weaned with stores very similar to those of adults (80–90%, depending on weaning age) (Fig. 3).

3.2. Iron status

There were significant age-related changes in serum iron, ferritin, and TIBC values with age, but no age-related differences in the percent saturation (Table 1). Serum iron and TIBC increased from neonates through early lactation, then declined to low values in weaned pups and adults (serum iron $F_{4,72}$=5.076, p=0.001, TIBC $F_{4,72}$=20.975, p<0.001). In contrast, serum ferritin levels were lowest in neonates, increased during lactation, and were highest in adults ($F_{4,72}$=13.728, p<0.001). In no case did sex influence parameter

Table 1
Mean (±S.E.) serum iron, ferritin, TIBC, and saturation values for harbour seals captured in Mont Joli, Canada in 2000 and 2001

Age class	n	Serum iron (μg dl^{-1})	Serum ferritin (ng ml^{-1})	TIBC (μg dl^{-1})	Saturation (%)
Neonates	15	369±37^{a,b}	14±6^{a}	572±19^{a}	65.1±6.0
Early lactation	15	497±36^{b}	35±6^{b}	599±19^{a}	80.6±6.0
Late lactation	14	475±38^{b}	29±7^{b}	582±20^{a}	81.7±6.2
Weaned pups	13	311±40^{a}	22±7^{a,b}	442±21^{b}	69.0±6.4
Adult females	13	260±38^{a,b}	70±7	357±21^{b}	68.9±6.4

Superscripts indicate that values were similar between age classes.

values. When we examined if iron status had an impact on blood oxygen stores, we found that animals with elevated saturation rates had lower oxygen stores than expected for their age class ($F_{1,39}$=8.407, p=0.007). Serum iron, ferritin, and TIBC values did not account for any additional variability in body oxygen stores.

4. Discussion

This work shows that there are clear differences in the physiological status at weaning of harbour seals and Steller sea lions, and suggests that these differences might be caused by differences in the pattern of growth and lipid accumulation in the two species. Like all phocids [1,2,5], harbour seal pups grew quickly, and deposited large lipid reserves during their short lactation period. Their rapid growth in body mass appears to outpace the development of new red cells, and as a result, oxygen storage capacity in the blood declines throughout the lactation period, when measured on both a lean and total body mass basis [16,18]. That this reduction in storage capacity is due to lagging red cell production rather than a decline in fluid volume is highlighted by the fact that plasma volume is similar in all age classes except the relatively hydrated neonates [16,18]. Since muscle oxygen stores do not increase during lactation, harbour seals are therefore weaned with oxygen stores that are less than 60% those of adult animals. Research on the physiological development of other phocid species has produced similar results: at the end of the postweaning fast, Weddell seals have oxygen stores that are 64% those of adults [11], Northern elephant seals (*Mirounga angust irotris*) 66% [9], hooded seals (*Cystophora cristata*) 62% [29], and grey seals (*Halichoerus gypus*) 67% [30]. The similarity of these values is remarkable, particularly given the large difference in the time between birth and independent foraging in these same species (32–82 days). We conclude that the pattern of physiological development reported here for harbour seals is a trait shared by all phocids, and therefore reflects constraints due to the capital provisioning strategy employed by most phocid females [1,2,31].

In contrast, Steller sea lions pups, like other otariids [3], grew more slowly over a much longer period of time, and deposited smaller lipid reserves than phocids [32]. Despite their slower growth rate, sea lions also showed a strong post-parturition anaemia, that was not relieved until 5 months of age, when pups swimming and diving activity increased [17,33,34]. As a result, blood volume and oxygen stores were relatively constant with age. This, in combination with increasing muscle oxygen stores, allowed juvenile Steller sea lions to increase their total body oxygen stores during the lactation period, so that oxygen stores were 69% those of adults when they began to dive, and 80–90% those of adults at weaning [17]. Data from other otariids suggest that the developmental pattern seen in Steller sea lions is characteristic of the group, and that most otariids are weaned with oxygen stores more similar to those of adults than seen in phocids [35–38].

Despite different patterns of physiological development, both harbour seals and Steller sea lions showed a strong early anaemia that coincided with the period of rapid growth and large gains in mass and lipid reserves. Developmental anaemia has been observed in many terrestrial species, and for rapidly growing neonates is typically attributed to an iron-poor milk diet [14,15]. Our examination of the iron status of harbour seal pups suggested their haematological development was also constrained by rates of iron intake during the period of most rapid growth. Iron stores (as indexed by serum ferritin) were low, and both TIBC and saturation levels were high in pups, as expected under conditions where iron is in high demand, but poorly available [39,40]. The similarly elevated saturation rates in lactating adult females may reflect the transfer of iron from tissue stores to milk. The remarkably high saturation rates (typical mammalian values are 20–30% [39,40]), and the negative correlation between saturation rates and oxygen stores further suggests that young juveniles may be constrained by both iron availability and the rate at which transport proteins can be produced [39,40]. While we do not yet have information on iron status in juvenile sea lions, northern fur seal (*Callorhinus ursinus*) pups have lower ferritin and higher TIBC values than do older animals [41], suggesting that the iron limitation observed in harbour seals may also exist in otariids. If iron limitation does contribute to the observed anaemia, then the postweaning increase in oxygen stores in harbour seals may result from intake of iron-rich prey items [15]. Similarly, supplemental foraging early in the lactation period may ameliorate early anaemia in Steller sea lions [33,34], just as it does in terrestrial species.

If iron kinetics influence oxygen store development, then it may also play a role in the postweaning fasts of phocid pups, a feature absent from the life history strategy of otariids [3]. Following weaning, many phocids fast on land for a period of days to weeks, and even those that do begin diving during lactation, such as harbour [42] and Weddell seals [43], apparently do not forage immediately upon weaning. Several studies have demonstrated that this fasting period is critical to proper physiological development, as body oxygen stores and the ability to regulate metabolic processes increase during the fast [9,30,44,45]. While increases in body oxygen stores during a period of fasting and mass loss are initially perplexing, we believe that this pattern can be explained by iron recycling. The majority (>80%) of a body's iron is stored in the erythron [46], and therefore changes in the size of the red cell pool has the potential to dramatically alter iron status. Because plasma volume is a constant proportion of body mass [16,18], as pups lose mass during the postweaning fast, absolute plasma volume drops. If red cells are not destroyed but retained in circulation, this will lead to an increase in HCT and blood volume, without any need for new cell production. For example, a 20% decline in the mass of harbour seal pups, as occurs in the weeks postweaning [42], would bring weaned pup HCT values to levels higher than those of adults, and increase blood volume from 12% to 14% of body mass. In addition, because iron is highly conserved [47], if some red cells are destroyed, their iron would then be available to support increases in muscle myoglobin content, as has been observed in fasting Northern elephant seal pups and emperor penguins [9,48].

Thus, the postweaning fast may allow phocid pups that rapidly gained mass (and blood volume) during the brief lactation period to reallocate iron stores, so that they can increase the size of oxygen stores relative to adult values during a period of mass loss. The similarity in relative maturity at the onset of foraging (~2/3 adult stores) across all phocids studied to date, suggests that there is a minimum threshold of maturity, below which foraging cannot be efficiently sustained. Since final completion of development only occurs postweaning, it likely requires additional nutritional input. Otariids, with their longer lactation period and slower growth rates are much more physiologically mature at weaning, and therefore may not require additional time to complete their physiological development.

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