

# The effect of maternal age and other factors on birth mass in the harbour seal

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We studied the effects of maternal age, maternal body mass at parturition, year of birth, birth date, pup sex, and developmental stage (as indicated by the presence of a foetal pelage called lanugo) on the birth mass of harbour seals (*Phoca vitulina*) on Sable Island, Nova Scotia, Canada. Between 1987 and 1992, mass was obtained on 330 newborns and 259 of their mothers. Birth mass was significantly correlated with maternal mass ( $r = 0.42$  for male pups;  $r = 0.32$  for female pups). Among pups that had shed their lanugo, males were significantly heavier at birth ( $11.4 \pm 0.09$  kg,  $n = 107$ ) than females ( $10.9 \pm 0.09$ ,  $n = 99$ ). Birth mass increased significantly with maternal age ( $n = 71$ , range 4–12 years) even after the effects of maternal mass and pup sex were statistically removed. Mean birth mass varied significantly among years, from 10.5 to 11.5 kg. Newborns averaged 12.8% of maternal mass at parturition ( $84.8 \pm 0.49$  kg). Most (84%) pups had shed their lanugo before birth. Pups born with extensive lanugo were born earlier in the season and weighed about 20% less than pups born without lanugo. These data suggest that pups born with lanugo may be less developed than pups that had shed their foetal coat. Young mothers (4 and 5 years old) produced most of the underweight, lanugo-covered pups.

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Nous avons étudié les effets de l'âge de la mère, de sa masse au moment de la parturition, de l'année de la naissance, de la date de la naissance, du sexe du rejeton et du stade de développement (tel qu'indiqué par la présence du pelage fœtal appelé lanugo) sur la masse à la naissance chez des Phoques communs (*Phoca vitulina*) dans l'île des Sables, Nouvelle-Écosse, Canada. Entre 1987 et 1992, la masse a été mesurée chez 330 nouveau-nés et 259 mères. La masse à la naissance était en corrélation significative avec la masse de la mère (rejetons mâles,  $r = 0,42$ ; rejetons femelles,  $r = 0,32$ ). Parmi les rejetons qui avaient déjà rejeté leur pelage fœtal, les mâles étaient significativement plus lourds à la naissance ( $11,4 \pm 0,09$  kg,  $n = 107$ ) que les femelles ( $10,9 \pm 0,09$ ,  $n = 99$ ). La masse à la naissance augmentait significativement en fonction de l'âge de la mère ( $n = 71$ , étendue 4–12 ans), même après avoir apporté une correction tenant compte des effets de la masse de la mère et du sexe du rejeton. La masse moyenne à la naissance a varié significativement d'une année à l'autre, de 10,5 à 11,5 kg. La masse des nouveau-nés représentait en moyenne 12,8% de la masse de la mère au moment de la parturition ( $84,8 \pm 0,49$  kg). La plupart des rejetons (84%) avaient rejeté leur pelage fœtal avant la naissance. Les petits nés avec une couche importante de lanugo naissaient plus tôt dans la saison et leur masse était d'environ 20% inférieure à celle des petits nés sans lanugo. Ces données indiquent que les petits nés avec leur pelage fœtal sont probablement moins développés que ceux qui naissent sans pelage fœtal. Les mères plus jeunes (4 et 5 ans) sont celles qui produisent le plus de petits à masse inférieure à la normale, encore recouverts de leur lanugo.

[Traduit par la rédaction]

## Introduction

Birth mass has often been used as an indirect measure of prenatal maternal reproductive effort (Millar 1977; Martin and MacLarmon 1985; Oftedal 1985; Kovacs and Lavigne 1986; Read and Harvey 1989). Birth mass has been shown to increase with increasing maternal body mass both across (Leitch et al. 1959; Millar 1977; Blueweiss et al. 1978; Robbins and Robbins 1979; Oftedal 1985; Kovacs and Lavigne 1986) and within species (Costa et al. 1988; Boyd and McCann 1989; Iverson et al. 1993). However, age, parity, nutritional condition, and social rank of the mother, and birth date and sex of the offspring can affect birth mass in mammals (Guinness et al. 1978; Reiter et al. 1981; Clutton-Brock et al. 1984; Michener 1989; Boyd and McCann 1989; Trites 1991).

The effects of early reproduction on maternal fitness depend on the viability of offspring produced. If a young female is small, her offspring may also be small (Clutton-Brock et al. 1984; Trites 1991) and may have a low probability of survival (Van Ballenberghe and Mech 1975; Guinness et al. 1978; Calambokidis and Gentry 1985). Although this may simply be a result of small body mass, it may also reflect the lack of maternal experience (Reiter et al. 1981; Trites 1991) or may be a trade-off between maternal growth and reproduction in species that continue to grow after beginning to reproduce (Reiss 1989). If offspring do not survive, young or small mothers may still gain maternal experience that could enhance the success of future offspring. This may be important in long-lived species such as pinnipeds, where premature separation of mother and pup often results in high pup mortality

TABLE 1. Dates and numbers of newborn harbour seal pups weighed on Sable Island, 1987–1992

Year	Number		Sex ratio	Birth mass, kg (mean $\pm$ SE)	Mean birth date in May	Sampling dates
	M	F				
1987	26	18	1:0.7	10.6 $\pm$ 0.30 $ab$	21	May 20–28
1988	31	46	1:1.5	10.5 $\pm$ 0.15 $a$	26	May 22 – June 7
1989	12	26	1:1.9*	11.5 $\pm$ 0.21 $c$	22	May 11–30
1990	21	16	1:0.8	11.0 $\pm$ 0.18 $bc$	22	May 17 – June 1
1991	34	30	1:0.9	11.0 $\pm$ 0.13 $b$	21	May 15 – June 3
1992	42	28	1:0.7	11.1 $\pm$ 0.12 $bc$	25	May 18 – June 1

NOTE: Year followed by the same letter are those in which mean birth mass was not significantly different at the 5% level. M, males; F, females.

\* $\chi^2 = 5.2$ ,  $p = 0.02$ .

(Le Boeuf and Briggs 1977; Reiter et al. 1981; Boness et al. 1992). Like other pinnipeds, harbour seals (*Phoca vitulina*) are long-lived, iteroparous mammals that begin reproduction while they are still growing. Thus, there are theoretical grounds for expecting that pinniped mothers of different body mass or age might invest differently in their offspring during gestation. Although a few harbour seal females give birth at 4 years of age, the proportion of females that give birth increases rapidly to about age 7 and remains relatively stable thereafter (Boulva and McLaren 1979).

In general, there has been little attempt to determine the factors that affect birth mass in harbour seals (but see Boulva 1975). One reason for this is that there are few direct estimates of birth mass in this species (Klinkhart 1969, cited in Newby 1973; Bigg 1969; Fisher 1952). Because of the difficulty in capturing harbour seals shortly after birth in most populations, previous estimates (Vaughan 1978; Boulva and McLaren 1979; Markussen et al. 1989) were extrapolations from relationships between foetal mass and foetal age or between body mass and pup age. In other studies, pup ages were unknown or not specified, therefore the accuracy of the estimates is unknown (Newby 1973; Drescher 1979; Härkönen and Heide-Jorgensen 1990).

Although most other phocid seals are born with a foetal pelage known as lanugo (Ling 1970; Ling and Button 1975) that assists in thermoregulation, harbour seal pups are usually born without this pelage, as they have undergone a prenatal moult (Ling and Button 1975; Oftedal et al. 1991). On Sable Island, 12–26% of harbour seal pups are born with a considerable amount of lanugo (Boulva and McLaren 1979; Oftedal et al. 1991). It has been suggested that lanugo-covered pups represent near-term, aborted fetuses, pups born prematurely before the normal pupping period, and those born early in the breeding season (Bishop 1968; Boulva and McLaren 1979). These and our own observations suggest that pups born with lanugo may be less developed at birth than those born without and, therefore, may serve as another index of the quality of the pup produced by a female.

In this study, we investigated the relationships of harbour seal pup mass and developmental stage at birth (as indicated by the presence of lanugo) to maternal mass and age. Our hypothesis was that heavier and older mothers would produce heavier, better developed pups. We also examined the effects of pup sex, birth date, and year of birth on body mass of newborns.

## Materials and methods

Data were collected in May and June 1987–1992 during the course of long-term population studies of harbour seals on Sable Island, Nova Scotia, Canada (43°55'N, 60°00'W). Harbour seals give birth on both the north and south beaches of the island. Our studies have been conducted over a 24-km stretch of the north beach (only 13 km in 1987) where females and pups are distributed in small groups, so that capture in one group does not disturb mothers and pups in other groups. Between 550 and 600 pups were born on the island each year during the study, with about 60% of these births occurring on the north beach (W.T. Stobo, personal communication). Pupping normally begins about 10 May and the last few pups are born late in the first week of June, so pupping covers a period of about 30 days (Boulva and McLaren 1979).

Each day throughout most of the pupping period, all newborn pups in the study area were sexed and tagged in the hind flipper with an individually numbered Rototag. Most days during the same period, mothers and their newborn pups were captured and weighed as described by Bowen et al. (1992a). Body length was not measured because in our experience it is not possible to obtain accurate or repeatable measurements on live seals without the use of a sedative. We used several criteria in deciding if a pup was a newborn. In most cases, newborns were still wet with birth fluids, and pieces of the amnion clung to the pup or fresh blood stained its coat and the birth site, indicated by a patch of blood-stained sand and shed lanugo. Newborns also had difficulty holding their head erect and displayed an awkward "gait."

Only mother–pup pairs captured on the day of birth ( $n = 302$ ) or the day after birth ( $n = 28$ ) were included in this study. We included mothers and their pups measured at 1 d post partum to maximize the number of known-age females in the analysis. In these pairs, body mass was adjusted to mass at parturition by subtracting the average daily mass gain of pups (0.5 kg/d) from pup mass at day 1 and adding the average daily mass loss of females (1.7 kg/d) to female mass at day 1. The mean rates of mass change used in these adjustments were estimated from a sample of 12 pups and 9 mothers weighed at birth and again at 2 d post partum.

Seventeen mothers were studied during more than 1 year. When this occurred, information from only 1 year was randomly selected and included in the analyses. Although not used elsewhere in the analyses, longitudinal data from 16 of these females were used to construct Table 3.

The percentage of lanugo covering the body of newborns was visually estimated. Pups with no lanugo and those with trace (<5%) amounts (usually on the lower back) were classified as having no lanugo. Of the pups in this first category, 87% had no lanugo and 13% had only traces. Pups covered with more than a trace of lanugo were further subdivided into those having a moderate amount of lanugo (less than 50%) and those having extensive lanugo (50% or more).

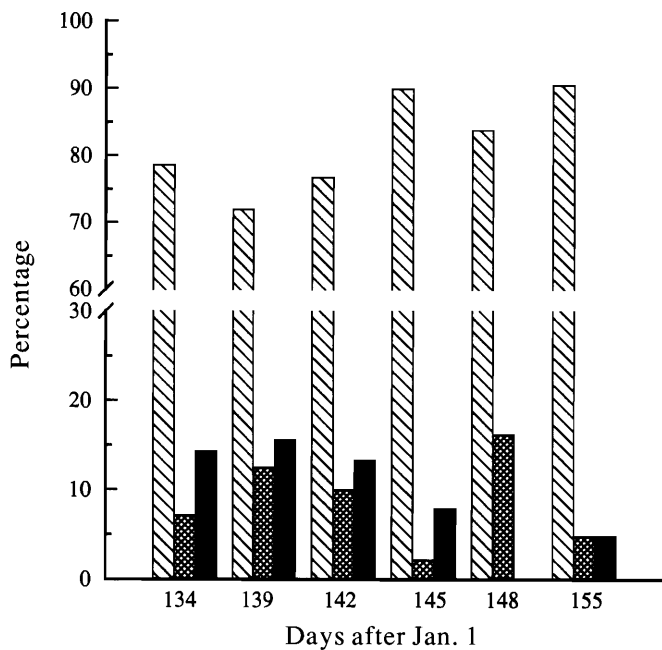


FIG. 1. Percentage of harbour seals on Sable Island born without lanugo (hatched bars), with <50% lanugo (cross-hatched bars), and with ≥50% lanugo (solid bars) in relation to birth date (expressed as days after January 1) between 1987 and 1992. Labels on the x axis represent the midpoints of the following groups of days: 130–137, 138–140, 141–143, 144–146, 147–149, 150–160.

Each year since 1978 most of the harbour seal pups born on Sable Island were tagged shortly after birth (W.T. Stobo and B. Beck, Bedford Institute of Oceanography, Dartmouth, N.S., personal communication). Many of these seals lost their tags before reaching maturity, but some have retained their tags for more than a decade. Thus, the ages of a subset of captured mothers were known.

All statistical analyses were done using STATGRAPHICS 5.2 (Statistical Graphics Corporation, Rockville, Md.). We used Type III sums of squares in the analysis of covariance models to determine the significance of factors.

## Results

### Interannual variation

The period over which births were sampled varied somewhat between years, but covered the main part of the pupping period in all years (Table 1). We sampled between 10 and 25% of births on the north beach each year.

Departure from a sex ratio of 1:1 was found only in 1 of the 6 years: in 1989, females significantly outnumbered males in the sample (Table 1). Over all years, the sex ratio of newborns (166 males : 164 females) did not differ from 1:1 ( $\chi^2 = 0.01$ ,  $df = 1$ ,  $p = 0.91$ ).

Maternal body mass at parturition did not differ significantly among years (ANOVA,  $F_{[5, 253]} = 1.6$ ,  $p = 0.17$ ). Mean birth mass differed significantly among years after the effect of maternal body mass at parturition was removed (ANCOVA,  $F_{[5, 246]} = 3.5$ ,  $p = 0.005$ ; Table 1). The maximum difference in mean birth mass between years was 10%. The mean birth mass over all years was  $10.9 \pm 0.07$  kg ( $n = 259$ ), or 12.8% of maternal mass at parturition (mean =  $84.8 \pm 0.49$  kg,  $n = 259$ ). Mean birth mass of harbour seals was not correlated with mean birth date between 1987 and 1992 ( $r = -0.26$ ,  $p = 0.62$ ; Table 1).

TABLE 2. Birth mass (kg) of male and female harbour seals as a function of percentage of lanugo

% lanugo	Males		Females	
	Mean	SE	Mean	SE
0–5	11.4 (107)	0.09	10.9 (99)	0.09
6–49	10.8 (10)	0.30	10.2 (5)	0.42
50–100	9.2 (10)	0.30	9.3 (13)	0.27
Total	11.2 (127)	0.11	10.7 (117)	0.12

NOTE: Numbers in parentheses are sample sizes.

### Timing of births within season

Birth mass was significantly correlated with birth date only in female pups born in 1992 ( $r = 0.39$ ,  $n = 28$ ,  $p = 0.04$ ). Overall, there was no correlation between birth mass and date of birth in male ( $r = 0.03$ ,  $n = 166$ ,  $p = 0.66$ ) or female ( $r = 0.006$ ,  $n = 164$ ,  $p = 0.94$ ) pups. Maternal body mass at parturition showed no trend with date of birth within each year or overall for mothers of male ( $r = 0.07$ ,  $n = 135$ ,  $p = 0.45$ ) or female ( $r = -0.04$ ,  $n = 124$ ,  $p = 0.62$ ) pups. Within a given age or age group (i.e., 4–5, 6, 7, 8, and 9–12 year olds) there was also no correlation between maternal mass at parturition and birth date of pups ( $n = 17, 12, 12, 11$ , and  $19$ ,  $p = 0.61, 0.60, 0.18, 0.48$ , and  $0.16$ , respectively).

Bishop (1968) suggested that pups with lanugo present at birth were born early in the breeding season. To examine this, we compared the temporal distribution over the pupping season of newborn pups in each of the three birth-coat categories. The percentage of pups born with 50% or greater lanugo decreased from about 15% early in the season to only 4.8% near the end of the pupping period (Fig. 1). Pups with extensive lanugo were born significantly earlier in the pupping season than those with little or no lanugo ( $\chi^2 = 18.2$ ,  $df = 10$ ,  $p = 0.05$ ).

### Birth mass in relation to birth coat and sex of pup

The sex ratio of 281 newborn pups was independent of birth-coat category ( $\chi^2 = 0.73$ ,  $df = 2$ ,  $p = 0.69$ ) and did not differ from 1:1 within each category (0–5% lanugo, 114 male : 117 female; 6–49%, 13:10; 50–100%, 12:15) or overall (139 male : 142 female;  $\chi^2 = 0.02$ ,  $df = 1$ ,  $p = 0.86$ ).

A two-way ANCOVA using maternal body mass at parturition as the covariate showed that pup birth mass differed significantly among the three birth-coat categories ( $F_{[2, 237]} = 36.3$ ,  $p < 0.001$ ; Table 2) but not between males and females ( $F_{[2, 237]} = 2.1$ ,  $p = 0.145$ ). Pups born with more than 50% lanugo were lighter than those that had moulted prior to birth by 17 and 23% in females and males, respectively. Although there was no significant interaction between pup sex and lanugo category ( $p = 0.44$ ), we felt that the order of magnitude difference in sample size among birth-coat categories and the small sample sizes of two of the categories may have obscured sex differences in birth mass (Table 2). To examine this possibility, we ran a one-way ANCOVA using only those pups with <5% lanugo, again controlling for the effect of maternal mass on pup birth mass, and found that male pups ( $11.4 \pm 0.09$ ,  $n = 107$ ) were significantly heavier than females ( $10.9 \pm 0.09$ ,  $n = 99$ ) pups ( $F_{[1, 203]} = 14.5$ ,  $p < 0.001$ ).

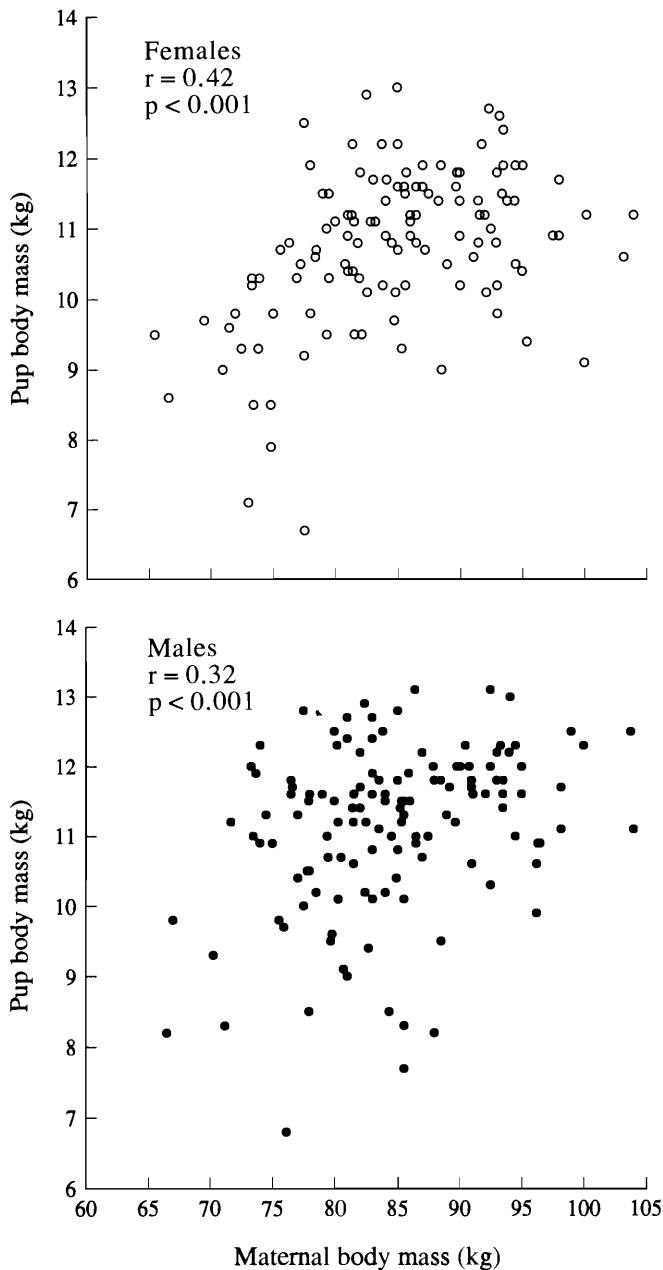


FIG. 2. Birth mass (kg) of 124 female and 135 male harbour seal pups at parturition plotted against maternal mass (kg).

#### Maternal mass and age

Birth mass for both males and females was positively correlated with maternal mass at parturition ( $r = 0.32$ ,  $p < 0.001$  and  $r = 0.42$ ,  $p < 0.001$ , respectively; Fig. 2). However, the correlations between maternal mass and birth mass did not differ significantly between male and female pups ( $p = 0.30$ ).

Birth mass increased significantly with increasing maternal age (Fig. 3), even after the effects of maternal mass and pup sex were statistically removed in a two-way ANCOVA ( $F_{[4,61]} = 7.1$ ,  $p < 0.001$ ). Pups of young mothers were significantly more likely to be born with lanugo than those of older mothers ( $\chi^2 = 17.7$ ,  $df = 4$ ,  $p = 0.001$ ). Because of small

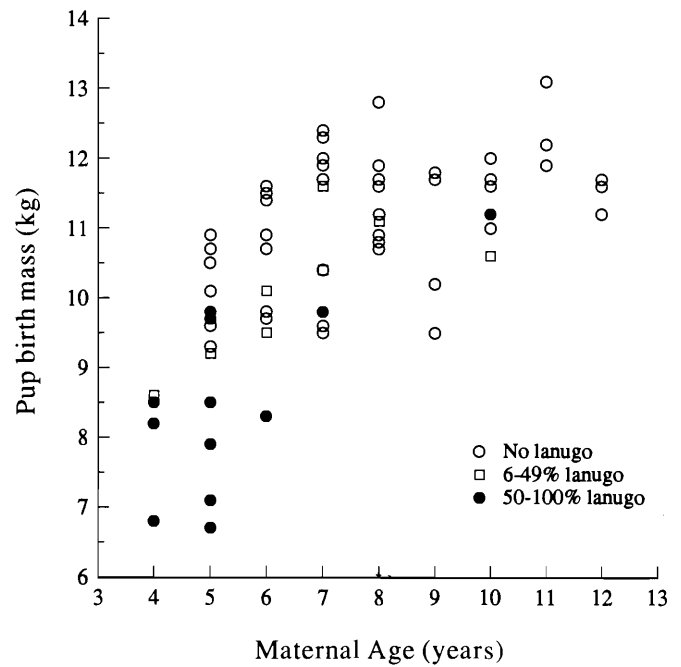


FIG. 3. Birth mass (kg) of harbour seals born with no lanugo ( $n = 51$ ),  $<50\%$  lanugo ( $n = 8$ ), and  $\geq 50\%$  lanugo ( $n = 12$ ) as a function of maternal age.

sample sizes, we combined the 6–49 and 50–100% lanugo categories and pooled ages 4, 5, and 9–12 into 4–5 and 9–12 age categories for this analysis.

Data from 16 known-age females indicated that the occurrence of lanugo-covered newborns was most likely a function of maternal age rather than a characteristic of individual mothers (Table 3). With one exception (female 7286), each of these females that in one year gave birth to a pup with moderate or extensive lanugo subsequently gave birth to a pup with substantially less or no lanugo.

#### Discussion

Harbour seals on Sable Island are relatively easily captured, unlike those in other populations. We usually approached females and their newborn pups on foot and invariably caught the pup without difficulty. Only rarely was it not possible to capture a female because she had entered the sea. Thus, it is unlikely that differential success in capturing females or their pups would have biased our results.

#### The effect of sex of pup on birth mass

In our study, male harbour seal pups averaged about 0.5 kg, or 4.6%, heavier than female pups at birth. In several previous studies of harbour seals (Boulva and McLaren 1979; Härkönen and Heide-Jorgensen 1990), no significant sex differences in birth mass were found. However, birth mass was not measured directly by Boulva and McLaren, but estimated from regressions of pup mass gain and estimated pup age. The small sample size (21) obtained by Härkönen and Heide-Jorgensen was not large enough for detection of a difference of 0.5 kg with high statistical power. By contrast, Klinkhart (1968 cited in Newby 1973) found that, on average, 34 female pups were heavier at birth than 34 males (13.2 vs. 12.8 kg).

TABLE 3. Percentage of the body covered by lanugo of pups born to 16 known-age harbour seal females captured in 2 or more years on Sable Island

Mother No.	Maternal age (years)									
	4	5	6	7	8	9	10	11	12	
1743	100	40								
H8171		100				0				
S6085		95	30							
S6115		50	0							
1580		50		30						
7286		0		10						
1549			20		0					
5218			5		0					
5154			0		0					
1422			0		0					
1733				90	0					
1512				25	5					
3122				0				0		
3040					0		0	0		
2937							0	0		
J9143							0			0

Sex differences in birth mass and postnatal growth rates of pinnipeds and other mammals have often been explained in terms of parental investment theory. Investment theory predicts that as a result of sexual selection, mothers should expend more resources on sons than on daughters insofar as males show greater variance in reproductive success than females and male reproductive success is dependent on large size (Maynard Smith 1980). Although variance in reproductive success appears to be greater in males than in females in many pinnipeds, based on evidence of polygyny (for recent reviews see Boness 1991; Le Boeuf 1991; Boness et al. 1993), studies relating male reproductive success to large body size (e.g., McCann 1981; Deutsch et al. 1990) are uncommon. However, in all otariids and some phocids, adult males are larger than females, as would be expected if large size provides a reproductive advantage to males.

Evidence from studies of otariids, which generally show that males are larger than females at birth, is consistent with investment theory (Trillmich 1986; Costa and Gentry 1986; Ono et al. 1987; Costa et al. 1988; Boyd and McCann 1989; Cappozzo et al. 1991; Trites 1991). By contrast, there is little evidence of sex differences in birth mass and growth rates among the phocids that exhibit size dimorphism (e.g., McCann et al. 1989; Le Boeuf et al. 1989; Campagna et al. 1992; Bowen et al. 1992b), suggesting a lack of differential maternal investment among phocids, contrary to the predictions of parental investment theory.

The harbour seal is a phocid species that exhibits little size dimorphism: in eastern Canada adult males are about 7% longer and 19% heavier than adult females (Boulva and McLaren 1979). The mating system of harbour seals is unknown, but some level of polygyny is suspected in this aquatically mating species (Sullivan 1981; Walker 1992). Whether a sex difference in birth mass reflects the action of sexual selection cannot currently be determined until more is known about the mating system of harbour seals. Also, conflicting data on the direction of sex differences in birth mass

of harbour seals and the relationship between birth mass and adult mass need to be clarified.

#### *Effects of maternal mass and maternal age on birth mass*

Maternal mass at parturition accounted for more than 50% of the variation in birth mass in several pinniped species (Costa et al. 1988; McCann et al. 1989; Iverson et al. 1993), but in harbour seals maternal mass accounted for less than 20% of the variation in birth mass of both male and female pups (Fig. 2).

Although maternal mass explained little of the variation in harbour seal birth mass, maternal age exerted a strong influence on birth mass. This suggests that reproductive "experience" may play a more important role in determining foetal growth rate and gestation length than maternal mass, as the older females presumably had greater maternal experience. Pups born to 4-, 5-, and 6-year-old females were significantly lighter than those born to older mothers, even after the effect of maternal mass had been statistically removed. Work by Boulva and McLaren (1979) indicates that all of the 4-year-old, most 5-year-old, and some 6-year-old harbour seal mothers are primiparous. If this is true of our sample, we can conclude that young, primiparous female harbour seals generally give birth to small offspring. This conclusion is tentative because the reproductive history of the females in our sample was not known. Trites (1991) found that primiparous northern fur seals (*Callorhinus ursinus*) were lighter and produced smaller young than multiparous females after the effect of maternal age had been removed, again suggesting the positive effects of prior maternal experience on birth mass.

Our data show that harbour seal pups which had moulted in utero were significantly heavier at birth than those which had not moulted or had only partially completed the moult (Table 2). Since the foetal pelage is shed just prior to normal term (Stutz 1966), harbour seal newborns that are covered with lanugo may be less developed at birth. In our study, 9 of 12 pups with more than 50% lanugo were born to 4- and

5-year-old mothers (Fig. 3), suggesting that young mothers tend to give birth to less developed, small pups. In harbour seals, foetal mass increases most rapidly near term (Boulva and McLaren 1979). In other mammals, low birth mass may be the result of a shortened gestation period, reduced foetal nutrition, or the interaction of these and other factors such as foetal genotype (McKeown et al. 1976).

Among mammals, small offspring often suffer higher mortality rates than larger ones (Guinness et al. 1978; Baker and Fowler 1992). If the same is true in the harbour seal, then young mothers, giving birth to small, less developed pups, may be less likely to leave surviving offspring than older females. Harbour seal pups of low birth mass, particularly those born with lanugo because they tend to be the lightest, might have a higher risk of mortality than pups of average birth mass, for several reasons. First, pups of low birth mass would have a high surface to volume ratio and thus may have to expend more energy to offset thermal losses. This effect may be especially pronounced if smaller pups are also born with less subcutaneous fat than normal pups. Harbour seal pups average about 11% body fat at birth, most of which is located in an insulating layer of blubber (Bowen et al. 1992a). In other mammals, prenatal adipose tissue deposition occurs during the latter stages of gestation (Hull 1975). Thus, pups born early may have less body fat than full-term foetuses. Both a high surface area to volume ratio and reduced insulation may be particularly disadvantageous in harbour seals, as pups usually enter a cold sea (where the rate of heat loss would be greatly increased) within hours of birth. Second, harbour seal newborns and those of other pinniped species have considerable difficulty in suckling over the first several days post partum (Tedman and Bryden 1979; Lawson and Renouf 1985; Kovacs 1987a, 1987b). If pups of low birth mass are less developed physically, they may have increased difficulty in both finding and remaining on the teat to suckle than do larger, more developed pups. This might retard growth during lactation, resulting in reduced weaning mass. Reduced weaning mass could be particularly significant in the case of harbour seals which, like all phocids, rely on stored energy during the transition to independent feeding (e.g., Ortiz et al. 1978; Worthy and Lavigne 1987; Muelbert and Bowen 1993).

Despite being significantly more likely to give birth to pups of low birth mass, young harbour seal females may benefit from early maternal experience, so that subsequent reproductive effort is more successful than it would have been otherwise (e.g., Reiter et al. 1981; Reiter and Le Boeuf 1991). Studies of postnatal growth and survival in relation to birth mass and maternal characteristics, such as age and parity, are needed to fully evaluate the costs and benefits associated with early reproduction in harbour seals.

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