PHYSICAL AND BEHAVIORAL DEVELOPMENT

OF NURSING HARBOR SEAL

(*PHOCA VITULINA*)

PUPS IN MAINE

By

John P. Skinner

B.S. Colorado State University, 2001

A THESIS

Submitted in Partial Fulfillment of the

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An Abstract of the Thesis Presented
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Compared to other phocids seals, the maternal investment strategy of the small bodied female harbor seal (*Phoca vitulina*) is complex. Females are unable to fast for the entire duration of pup rearing and are therefore reliant on resources in the vicinity of the pupping aggregation to continue provisioning their pup by mid-lactation. At the same time, harbor seal pups are highly active during lactation which increases energetic costs to the female but also offers an opportunity for females to influence the behavioral development of her pup. To understand how females maximize their pup's survival it is important to examine both the physical and behavioral development of harbor seal pups. The goal of my research was to describe the morphological development and ontogeny of diving behavioral for harbor seal pups in Maine in respect to the potential factors influencing these two measures of maternal investment. I conducted my research at pupping sites in the vicinity of Stonington, Maine. During two seasons, 156 pups were captured, weighed and measured, and equipped with identification tags. Birth dates were

estimated for all individuals and a subset of animals received VHF radio transmitters and time-depth recorders (TDRs) in order to monitor movements, activity, and diving behavior. Pups were monitored using telemetry and were recaptured opportunistically to recover TDRs and measure growth. There was no difference in the timing of births between years and the mean pupping date was found to be May 23rd (SE = 0.5). Mean birth mass was 11.1 kg (SE = 0.23) and mass gain rate averaged 0.45 kg/d (SE= 0.03). Pup mass gains were found to differ between years and decline late in the pupping season. Additionally, pup mass gain rates were found to be positively associated with increased 'in water' activity after controlling for temporal. Data from TDRs revealed that pups spent a large portion of time in water (61%) during lactation and dove up to 100 m near weaning. Activity and diving behavior was found to be influenced by pup birth mass, mass gain rate, age as well as the depth available and tide heights experienced by pups during TDR deployment. Maximal dive duration and dive depths were highly associated with bathymetry and this factor was most important in limiting pup diving depths early in lactation. The positive association between pup mass gain rate and activity is likely explained by the intermediary effects of female size and condition on both female attendance and pup growth. Although the lower mean mass gain rates in Maine compared to Canadian populations may be explained by differences in population status, this did not explain the lower range of values observed in this study. Resource limitations in the vicinity of pupping sites may provide an explanation for lower pup development and the significant decline in mass gain rates late in the pupping period in this study.

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PREFACE

For any species, the goal of a reproduction is to maximize fitness. At the two extremes, a species may invest in the number of offspring ('r' selected) or focus energy into the quality of few or even one offspring ('K' selected). For 'K' selected species, reproductive strategies can be further subdivided based on the amount investment made in physical versus behavioral development of the offspring to ensure its survival. Especially in mammals that have a period of post-partum milk provisioning, females are capable of enhancing both physical condition and behavioral readiness of their young. Milk provisioning allows young to grow to a more capable size under the protection of the female but also provides fat reserves that serve to buffer them from starvation as they learn to forage and achieve a positive energy balance after weaning. Young that are sufficiently precocial during the lactation period may learn from their mother. Having knowledge of their environment and the skills necessary to acquire resources may shorten the gap between weaning and nutritional independence and thereby reduce the amount of fat reserves required to prevent starvation. Depending on the foraging strategy, environmental conditions, and habitat available during the period of maternal care, a species must choose a suitable balance between these two forms of maternal investment in maximizing the survival of their young.

Unlike terrestrial mammals that may choose to reside in suitable foraging habitats during the birthing period, female seals must give birth to pups on land in areas that are not necessarily adjacent to optimal foraging sites. To cope with this shift in distribution during pupping season, some phocids have evolved very short periods of milk provisioning and fast for the entire duration of lactation (*e.g.,* hooded seal, gray seal, harp

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seal). These species have relatively sedentary pups that have no opportunity to learn from

their mother. In other phocids (*e.g.,* Weddell seals, bearded seals, ringed seals, and harbor

seals), females continue to rely on resources at the pupping site and typically have

extended periods of maternal care. Pups of these species enter the water and spend time

with the female before the end of lactation – potentially observing and learning from her

as she forages.

The harbor seal has exceptionally precocial young among phocids. Pups are

encouraged by the female to enter the water within minutes of birth and remain active

throughout the nursing period. They also quickly learn to dive and follow their mother

and by the end of a three week lactation period they become highly skilled divers. Harbor

seal pups don't typically feed themselves and during the nursing period and are therefore

nutritionally dependent on their mother. In this species, maternal investment during the

nursing period has a physical and behavioral component that both likely contribute to the

pup's survival after weaning.

In the first chapter of my thesis, I examine the characteristics of physical

development for harbor seal pups from birth to weaning in Maine. Using birth mass and

mass gain rates as indices of energetic maternal investment, I first compare harbor seal

pups in Maine to other populations in the Northwestern Atlantic. A difference in physical

development of pups in Maine after considering the influences of population status,

disturbance, and habitat may indicate a difference in resources or maternal investment

strategy by female in Maine. Secondly, I examine potential influences of habitat, pup

activity, and female attendance on the development of pup fat reserves (*i.e.,* mass gain

rate) during the lactation period.

I explore the ontogeny of pup diving behavior during the lactation period in my second chapter. Here I examine how observed pup behavior is influenced by their physical development, morphology, age and the characteristics of their environment. Through the understanding of how these factors influence pup diving development, I hope to provide an improved understanding of how pups behaviorally transition to an independent forager.

To fully understand how female harbor seals ensure their pups' survival it may be important to consider both the physical and behavioral components of maternal investment during the nursing period.

CHAPTER 1

THE TIMING OF BIRTHS AND PHYSICAL DEVELOPMENT OF NURSING HARBOR SEAL (*PHOCA VITULINA*) PUPS IN MAINE

INTRODUCTION

The harbor seal (*Phoca vitulina*, Linnaeus 1758) has a worldwide distribution, occurring in temperate, sub-arctic and arctic waters of the northern hemisphere. This species is generally found in shallower water associated with the coastal continental shelf and, in some cases, freshwater rivers and lakes (Mansfield 1967). There are likely four subspecies of harbor seal, including the Pacific (*P.v. richardsi*), Western Atlantic (*P.v. concolor*), Eastern Atlantic (*P.v. vitulina*), and the Ungava harbor seal (*P.v. mellonae*) which is restricted to the Ungava lakes of Quebec, Canada (Smith *et al.* 1994). Although the Pacific harbor seal was originally divided into two subspecies based on morphology (Shaughnessy and Fay 1977, Bigg 1981), recent genetic evidence suggests that there is only one subspecies, *P.v. richardsi,* consisting of three distinct subpopulations (Burg 1999, Westlake and O'Corry-Crowe 2002). Because the harbor seal has an extensive distribution and persists in various climates it is ideally suited for examining phylogenetic and behavioral plasticity in response to regional differences in habitat.

The Western Atlantic subspecies (*P.v. concolor*) ranges from Greenland to the eastern arctic coasts of Canada and south along the Atlantic coast of the United States (Mansfield 1967, Boulva and McLaren 1979, Payne and Selzer 1989, Baird 2001). Less frequently harbor seals are seen along the mid-Atlantic coast (Schneider and Payne 1983) and stranded animals are occasionally found as far south as Florida (*Anonymous* 2005). In

the U.S and Canada, harbor seals were historically perceived as a threat to fisheries and bounties were commonly offered. As a result, the harbor seal was intensely hunted and by the mid-1900's most pupping aggregations south of Maine were extirpated (Allen 1942, Katona *et al.* 1993). Unregulated killing continued in Canada until 1976, when the Department of Fisheries and Oceans implemented hunting regulations and discontinued the use of culling and bounties (Baird 2001). In 1972, the U.S. Congress passed the Marine Mammal Protection Act (MMPA) which banned the killing of harbor seals and other marine species in U.S. waters.

Based on scarce trend data over its entire range, the overall status of *P.v. concolor* appears to be improving despite some localized declines in northern populations (Baird 2001). Aggregations in Greenland are apparently stable, however, this hunted population historically persisted at low numbers (Teilmann and Dietz 1994). In the northern parts of Canada, there are no current data on abundance (Baird 2001). As in Greenland, these northern harbor seal pupping sites appear to be small and widely dispersed. In the 1970's, the population in the Canadian arctic was thought to be in decline as a result of overexploitation by aboriginal people (Mansfield, 1967, Boulva and McLaren 1979). Recent counts in the Saint Lawrence River Estuary (SLR) are lower than previous estimates suggesting a decline in numbers, although the survey methods were not standardized between periods (Baird 2001). During the breeding season, the pupping population on Sable Island has declined substantially since 1991 (Bowen *et al.* 2003), where births fell from approximately 600 pups in 1990 to 18 in 1999. This island may soon cease to be a pupping or breeding site for harbor seals (Bowen *et al.* 2003, Lucas and Stobo 2000).

In the Gulf of Maine, at the southern end of the breeding range for *P.v. concolor*, populations have steadily increased in the past few decades. According to Fowler and Stobo (2005), the population in the Bay of Fundy, New Brunswick increased at an annual rate of 9.3% between 1986 and 1995. The adjoining Maine aggregations had similar increases. The first Maine population surveys conducted (near the time when the MMPA was passed) offered a minimum estimate of 5,785 seals in Maine (Richardson 1976). In recent decades, standardized surveys have shown increasing trends (Gilbert *et al.* 2005). The latest minimum count of 38,014 suggested a 28.7% total increase and 6.6% annual increase in the Maine population from 1981 to 2001 (Gilbert *et al.* 2005). Despite these trends, the overall geographic distribution has not changed for this subspecies in the past half century (Payne and Selzer 1989). Pupping is believed to have historically occurred in southern New England (Katona *et al.* 1993) but Maine is currently recognized as the southern extent of the pupping range for *P. v. concolor* (Rosenfeld *et al.* 1988, Gilbert pers. comm.). More recently, pupping has been observed in Massachusetts (Waring *et al.* 2006) and a newborn was reported on Long Island, NY (Durham *et al.* 2005).

The harbor seal is a resident of Eastern Canada and Maine throughout the entire year (Boulva and McLaren 1979, Katona *et al.* 1993). It has been previously described as non-migratory (Bigg 1981) however there are apparent seasonal north-south shifts in the population distribution. Decreases in the harbor seal numbers in Canada are concomitant with increases in the southern New England population during the winter (Rosenfeld *et al.* 1988). Additionally, adult harbor seals radio tagged in Massachusetts during the winter moved to waters off the coast of Maine during the following spring (Waring *et al.*

2006). The absences of some radios during relocation efforts in Maine suggest that some adults may have exhibited seasonal movements to unsearched sites.

Within a geographical area, the timing of harbor seal pupping tends to be synchronized. This allows pups to be born when conditions are most favorable for survival (Enders 1981). After mating, the female harbor seal, like all pinnipeds, experiences delayed implantation (Fisher 1954). This is the mechanism by which a twelve-month reproductive cycle can be maintained, since mating occurs shortly after females wean their pups and the active gestation period is only 36 – 39 weeks (Bigg and Fisher 1974). Implantation is triggered by localized proximate cues (Boyd 1991) and for the harbor seal it is thought to be primarily regulated by photoperiod (Tempte 1991, Tempte 1994, Gardiner *et al.* 1999). This explanation has been shown to account for the generally later pupping dates observed in populations from south to north, which is consistent with a lag in the timing of critical day length cues (Bigg 1969*a*, Tempte *et al.* 1991).

The precise critical day length required for embryo implantation is thought to be genetically adaptive. The Pacific harbor seal (*P.v. richardsi*) was found to undergo implantation when exposed to a critical day length 2.5 hrs longer than required for *P.v. vitulina* (Tempte 1994). A two month later peak in pupping observed in Puget Sound, Washington compared to outer coast populations at the same latitude was found to coincide with a genetic difference between these populations (Lamont *et al.* 1996). In contrast, Tempte *et al.* (1991) found no correspondence between latitude and timing of births for *P.v. vitulina* for pupping areas stretching from 50° N to 80° N latitude. Many of these sites exhibit genetic sub-structuring (Coltman *et al.* 2002) and may have a unique

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implantation response to photoperiod. This genetically flexible response to photoperiod may allow birthing to take place when the resources are plentiful over the long-term; however, environmental conditions can vary substantially between years.

Within a distinct pupping area, there are year to year differences in the timing of births generally thought to be associated the condition of pregnant females. Boyd (1996) saw significantly longer gestation lengths for Antarctic fur seals, *Arctocephalus gazella*, during years of reduced food abundance. Additionally, the mean pupping date was found to be 7 days later for harbor seals on Sable Island after a population decline, thought to be caused by reduced recruitment due to increased shark predation or competition for resources with an increasing gray seal (*Halichoerus grypus*) population (Lucas and Stobo 2000, Bowen *et al.* 2003). It was acknowledged that a shift in age distribution toward older females may have also contributed to the observed change in parturition dates since older females have been shown to give birth later in the pupping season (Ellis *et al.* 2000).

After reaching sexual maturity between 4 and 6 years of age, female harbor seals give birth to a single pup annually (Boulva and McLaren 1979). Harbor seal pups are well developed at birth and with the encouragement of the mother will enter the water within minutes of being born (Newby 1973). They remain active in the water during the lactation period with and without the female but do not attempt to feed themselves (Muelbert and Bowen 1993). Nursing pups are, therefore, dependent on milk provisioning from the female for growth and accumulation of fat reserves, which are vital for survival after weaning (Harding *et al.* 2005). Harbor seal pups typically shed their fetal coat (*i.e.* lanugo) prior to birth but in some cases this fur can persist for up to a 14

days post-partum (Boulva and McLaren 1979). Pups with lanugo are smaller than non-lanugo pups and are more commonly seen early in the pupping season (Boulva and McLaren 1979, Bowen *et al.* 1994, Ellis *et al.* 2000). This trait is generally considered to be an indicator of underdevelopment at birth and is more often seen in pups of smaller, younger mothers. On Sable Island, 47% of births for females 4-6 years old were lanugo pups while there were no lanugo pups born to females older than 10 years of age (Ellis *et al.* 2000). Variations in other newborn characteristics and developmental traits can be attributed to the characteristics of the parturient female (Bowen *et al*. 1992, 1994, 2001, Ellis *et al.* 2000). Both maternal postpartum mass and female ages were found to be positively correlated with pup birth mass explaining 20% and 54% of the variation in this trait respectively (Ellis *et al.* 2000). After controlling for female mass, younger females, 4-6 years old had significantly smaller and less developed pups at birth. Additionally, the rate of mass gain in pups is highly influenced by the mass of females (Bowen *et al.* 2001*a*) because larger females have more fat reserves available to use in milk production (Oftedal *et al.* 1987).

An early account of harbor seal biology in Maine reported that newborn pups weighed 9 kg, measured 86 cm in length and 51 cm in girth (Hunt 1948). Sample size, deviation, and the method used to determine pup ages were not given. There are no recent data for *P.v. concolor* pupping traits in the Gulf of Maine but considerable information has been provided by research in other localities. On Sable Island, pups weighed 10.9 kg (SE = 0.09) at birth and gained mass at 0.6 kg/d (SE = 0.01) while nursing (Bowen *et al.* 2001*a*). Newborn males were significantly heavier than females. In the St Lawrence River pups weighed 11.1 kg (SE = 0.22,) and gained mass at 0.54 kg/d (SE = 0.14, Dubé

et al. 2003). Pupping traits are highly variable between individuals, with reported birth masses ranging from 6.5 kg to 14.2 kg on Sable Island (Ellis *et al.* 2000) and mass gain rates varying from 0.11 to 0.88 kg/d in the St Lawrence River Estuary (Dubé *et al.* 2003). Measures of standard length have been less frequently reported. Pups on Sable Island measured 76.6 cm (SE = 0.99, *n* = 3 yrs) at birth and by late lactation reached about 90 cm. Males tended to be larger than females; however the difference was not significant (Boulva 1975). Males have been shown to increase in standard length at 0.53 cm/d which was slower than the 0.63 cm/d reported for females, although the significance of this difference was not reported (Boulva and McLaren 1979).

Production of energy rich milk in mammals is energetically costly for females (Millar 1977, Oftedal 2000). Larger phocids fast for the duration of lactation and the amount of milk provided to the pup is entirely dependent on the female's fat reserves (Oftedal *et al.* 1987). This strategy allows females to acquire necessary reserves while in good foraging habitats and forgo foraging when at densely populated pupping sites with potentially less favorable habitat for foraging. The smaller-bodied harbor seal, however, has insufficient reserves to use this strategy. During the first 19 days of lactation, females lose 33% of their mass and 79% of their fat reserves (Bowen *et al.* 1992). More similar to Otariids than other Phocid seals, female harbor seals begin foraging by mid-lactation and may travel up to 45 km from pupping sites (Boness *et al.* 1994, Thompson *et al.* 1994). The timing of when a female begins foraging during lactation and the duration of each foraging bout is contingent on her postpartum mass and condition (Iverson *et al.* 1993, Arnbom *et al.* 1997). For larger females that can draw from accumulated fat reserves, it is more cost effective to put off foraging, since food acquisition and processing can account

for up to 70% of the daily energy expenditure in parturient females (Bowen *et al.* 2001*b*). Pup growth rate is likely affected by the increased energetic costs incurred by foraging females and the reduction in nursing opportunities while she is at sea. This may, in part, explain the lower mass rates observed in pups during late-lactation and be a major factor in limiting the overall growth of pups with smaller mothers (Bowen *et al.* 1992).

For a lactating female, the accessibility of foraging sites may affect her ability to provision her pup. Pupping sites are often located in protected bays and surrounded by shallow water (< 10m), while foraging areas are generally deeper (10-50m, Tollit *et al.* 1998). By mid-lactation, where a female chooses to relocate may be a compromise between needing to protect her pup from rough seas and large predators and finding suitable foraging habitat. Furthermore, if the pup is sufficiently capable, the female may choose to relocate it to ledges adjacent to deeper water to decrease commuting costs and time spent away from the pup. To my knowledge there has been no attempt to relate pupping site characteristics and neonatal behavior to physical development.

The duration of milk provisioning by harbor seal females and pup size at weaning has been less frequently studied because of the difficulty in capturing older pups and then positively determining that they are weaned. On Sable Island, harbor seals are less threatened by human activity and have offered researchers a better opportunity to measure pup development and weaning characteristics. Muelbert and Bowen (1993) followed known-age pups and estimated their weaning age based on the absence of the female, loss of body mass, and evidence that pups had not nursed by examining stomach contents and blood characteristics. They reported that weaning occurred at 24.1 (SE = 0.44) days post-partum (dpp) based on loss of mass, although all the methods they used

provided similar estimates. The length of lactation varied from 15 to 30 days for these pups. Later research on Sable Island confirmed these earlier findings; age at weaning was 23.9 dpp (SE = 0.24) with a range of 18 to 31 dpp (Bowen *et al.* 2001*a*). In the same study, pups were found to weigh 24.8 kg (SE = 0.26, range: 15.7 – 34.5 kg) at weaning.

Mass is likely to be one of the most important determinants of first-year seal survival (Harding *et al.* 2005, Hall *et al.* 2001). It is especially critical for pups to acquire sufficient reserves during lactation to afford them time to achieve a net positive energy balance before they starve after weaning. Size at birth, growth rate during lactation, and length of nursing together contribute to the mass of the pup at weaning. Although these developmental characteristics each may vary considerably between individuals, together they contribute to weaning mass, which can be thought of as an index of maternal investment in pup survival (Lee *et al.* 1991). Although pup growth rates for *P.v. richardsi* in British Columbia (Cottrell *et al.* 2002) were significantly lower (0.39 kg/d, SE = 0.03) than those reported for *P.v. concolor* (Dubé *et al.* 2003, Bowen *et al.* 2001*a*), longer nursing durations were observed in *P.v. richardsi* (32 d, SE = 1.5) which resulted in pups being weaned at a similar weight (23.6 kg, SE = 1.2). This compensation strategy has also been shown in the Sable Island population (Bowen *et al.* 2001*a*). Slower growing pups attended to by younger, lighter females were nursed longer and more consistently throughout lactation. As a result, pups that were born significantly lighter at birth, achieved similar weaning weights to those pups that were larger at birth due to having larger mothers. The relationship between postpartum female mass and pup weaning mass, which is more evident in phocids that fast during lactation (Kovacs and Lavigne 1986, Iverson *et al.* 1993, Arnbom *et al.* 1997), is apparently weaker in harbor seals. Foraging

during lactation apparently allows smaller females to prolong the provisioning of their pup and to compensate for their lower fat reserves.

As expressed by Laws (1993), the key to understanding the evolution and ecology of seals -- or any carnivore -- includes knowing the variation that a species exhibits throughout different parts of its range. Because the harbor seal is found across varied habitats and climates, this species is ideal for studying behavioral plasticity in maternal investment strategies. In contrast to previously studied *P.v. concolor* populations, the Maine harbor seal population – near the southern end of this subspecies pupping range – is currently characterized as having large, and rapidly growing pupping aggregations.

The goal of this research was to examine potential factors influencing the timing of births and pup developmental characteristics for the harbor seal. This was accomplished through two objectives. First, within this population, I set out to explain variations in mass gain rates using an index of site foraging quality (*i.e.* depth), pup mobility and activity, and female attendance. Second, I compared my estimates of the timing of births, birth masses, mass gain rates, and weaning masses for pups in Maine to values previously reported for populations in Canada.

STUDY AREA

I conducted this research in the vicinity of Stonington, Maine (44˚ 09.28' N, 068˚ 39.91' W) on and around the many inter-tidal ledges and small uninhabited islands to the east and south of Deer Isle, from here on referred to as Maine. The north and eastern boundary of the study area were marked by Crow Island and Egg Rock to the north and Marshall Island at the southeastern end of Jerico Bay. The western boundary was defined by West Mark Island Ledge near Stonington, The Brown Cow, and Scraggy Ledge along

the eastern edge of Penobscot Bay (Figure 1.1). Bathymetry within this 110 km^2 area is varied with a mean depth of 11.6 m and several channels reaching 62 m deep. The sea floor continues to fall in the surrounding 5 km where the mean depth is 16 m and reaches 105 m at a couple widely distributed locations. Substrate used for birthing by harbor seals in this area varies from the sandy beaches of uninhabited islands to craggy ledges that become submerged during the half-tide.

MATERIALS AND METHODS

Capture and Handling - Beginning on May 9th in 2004 and April 26th in 2005 my research crew and I searched adjacent to major haul-out sites each day and opportunistically captured newborn pups. Whenever possible, captures were carried out from a 4 m inflatable boat equipped with a 30-horsepower outboard motor using an aluminum dip net constructed from a 1 m diameter hoop attached to a 2.5 m pole for a handle. This method has been previously used in the Saint Lawrence River Estuary (Dubé *et al.* 2003) and British Columbia, Canada (Cottrell *et al.* 2002). When hauled out, females and pups were often mixed together in aggregations making it difficult to determine which females were together with their pups. By capturing pups in the water we could more easily determine if a pup was nursing since mother-pup pairs were found to generally maintain close proximity when swimming together. In many locations, sub-tidal rocks prevented operation of the outboard motor. In these cases (63% of total captures), we resorted to sneaking onto ledges and capturing pups by hand. This method also proved to be most effective for recapturing older pups that were aware of our boat and adept at evading the dip-net.
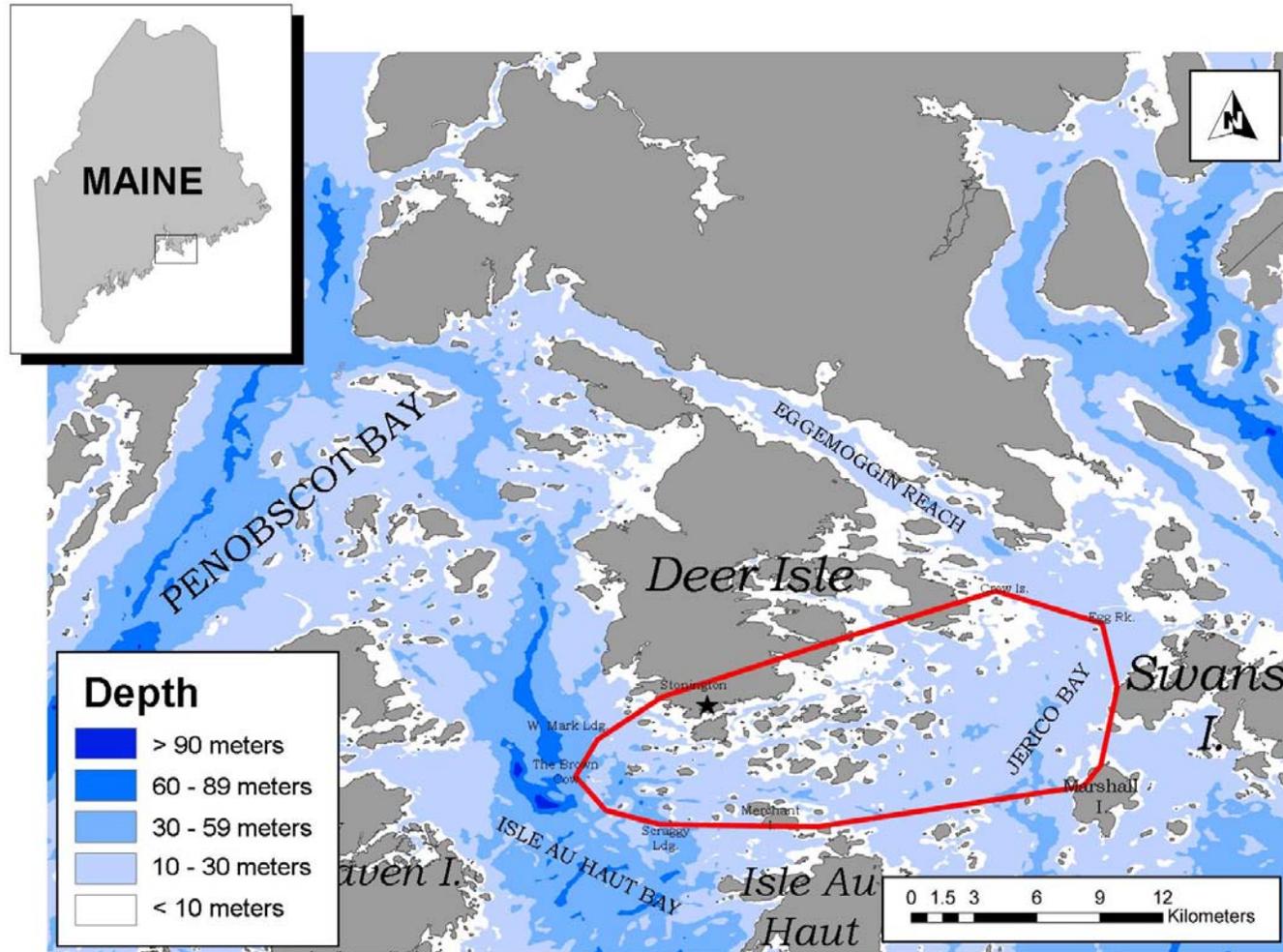
Figure 1.1. The location of harbor seal pup research conducted during 2004 and 2005. Ledges and islands within the study boundary (solid, red line) were searched for newborn pups between May and July during both seasons.

Once captured, pups were transferred to an anchored 7 m boat and restrained by hand or with a restraint board (Lapierre *et al.* 2004). During each initial capture, a genetic tissue sample was obtained using a hole-punch at less than 2 mm from the back edge of the left rear flipper. We marked each pup for permanent identification using a flipper tag that was installed in the right rear flipper webbing between the 2nd and 3rd digit (Flexi Supertags, Dalton supplies, England). Each tag was engraved with a three digit identification number and contact information to allow the seal to be reported if recovered. Pups were outfitted with a pyramid head tag (Dalton Supplies, England) to aid in identification during resighting (Hall *et al.* 2000). A subset of pups received a head mounted VHF radio transmitter (RMMT-4, LOTEK inc.) in place of the pyramid tag. Radio transmitters weighed approximately 200 g and less than the maximum recommended tag weight of 5% of animal mass (Cuthill 1991). To aid in visual identification of pups with VHF radio tags, we attached a yellow cattle identification tag with a two-digit number, in large print, on both sides of the radio. The radio transmitter or pyramid head tag was glued to the fur (Fedak *et al.* 1983) using five-minute epoxy (Devcon®) for the first two weeks in 2004 but was substituted with a cyanoacrylate based adhesive (Superbonder® 422 Adhesive, Loctite Canada Inc., Mississauga, ON, Canada) for the remainder of the study. The cyanoacrylate adhesive required no mixing or surface preparation, produced less heat while drying, and had a setting time of less than two minutes after application of an accelerant (Tak Pak® 7452 Accelerator, Loctite Canada Inc).

During all captures, we determined the sex of the pup and whether the fetal coat (lanugo) was still present. For pups having lanugo, the percent coverage was estimated. Each individual was weighed to the nearest 0.2 kg (Dillon, Model ED-2000, USA) and

axillary girth and standard length were measured to the nearest 0.5 cm (Scheffer 1967). In 2005, right-rear flipper length, zygomatic arch width, and protrusion of the upper canine teeth were measured to the nearest 1 mm and 2 12-ml vials of blood (one sample each of serum and plasma) were obtained from the extra dural vein using a *Vacutainer® System* (Becton, Dickinson and Co., Rutherford, U.S.A.) with a 2.5-inch, 18-gauge needle. Blood serum was later examined for cloudiness. Cloudy blood can be attributed to the presence of chylomicrons which are an indicator that the pup was fed in the past <4-6 hours (Bowen *et al.* 1985). During each capture, a pup was classified as nursing if either the mother was observed or if the blood serum was cloudy.

Because evidence of birth (*e.g.* meconium in stool, blood or placental material) was seldom observed, pup aging was generally accomplished by classifying the condition of the umbilicus. The presence of an umbilical cord indicates that a pup was born in the past 5 - 8 days (Boulva 1973). Fifty percent of pups lose their umbilicus by 6 dpp (Boulva and McLaren 1979). Pups were assigned to one of four categories using an extension of the criteria established by Boulva (1975): a.) evidence of birth = 0 dpp; b.) umbilicus long with pink, fleshy umbilical sheath sometimes with blood = 1 dpp; b.) firm sheath, < 3 cm and light pink or white = 3 dpp; c.) firm cord sheath, < 1 cm, white and often splitting at ends = 5 dpp or; d.) umbilicus absent, >5 dpp.

Precautions were taken to reduce the risk of pup abandonment by the attending female. Whenever possible, the mother was identified and pup vocalizations produced by the research team were used to encourage her to remain in the vicinity of the boat. Handling time was monitored and kept to the minimum required to accomplish processing and the objectives of this and concurrent research (Schreer in prep). Captures

were not conducted in high winds since high levels of background noise and rough water

can potentially hinder the mother's ability to locate and reunite with her pup following

release (Perry and Renouf 1988). After release, pups were monitored and the time was

noted when it reunited with its mother as indicated by a female-pup proximity or nose to

nose contact.

Pups were relocated using radio telemetry (Cochran and Lord 1963) at intervals of

between 1 and 6 days throughout the study period. During visual observations, the

presence or absence of the female was noted and the location of the pup was estimated

using the onboard WAAS-enabled GPS chart plotter or NOAA navigational charts. When

the pup was not physically located, the signal emitted from the head mounted radio was

monitored to determine if the pup was in water. Salt water attenuates the signal when the

radio is submerged, therefore, the pup was classified as "in water" if the signal was

intermittent or "hauled out" if the signal was uninterrupted for 5 min or more.

I used ArcMap™ version 9 (ESRI® Inc., Redlands, CA, USA) to analyze pup

location data. Straight line distances between visual relocations were summed and

divided by the number of days between capture and recapture to estimate pup daily

movement rate. Based on radio tracking data, nursing pups generally moved distances

less than 2 km from the location previously observed (unpublished data, this study).

During the period between initial capture and recapture, I defined the home range of each

pup to be the 2 km buffer around the minimum convex polygon of visual relocations. A

bathymetry grid of the study area was created by interpolating depths between contour

lines within the shape file 'BATHYM100' at a 30x30 m resolution. The 'BATHYM100'

shape file was downloaded from the Maine government website[1] and contained

bathymetry lines at 10 m intervals for the entire Gulf of Maine at a scale of 1:100,000.

Within a pup home range, the maximum depth in the BATHYM100 shape file was used

as an estimate of depth available (DA) to the female-pup pair.

Absence of a mother on multiple occasions is one indication that a pup is weaned

(Boulva and McLaren 1979, Muelbert and Bowen 1993). Because the reception ranges of

the radio transmitters were limited (~4 – 6 km) and female-pup pairs frequently moved

between different haul-out sites, pups were often not seen for several days at a time. To

account for this gap between observations, I considered the date of weaning to be the

mid-date between the last pup observation with its mother and the next date it was

observed alone. The pup was only considered weaned if it was confirmed to be alone on

at least one additional occasion. Furthermore, if the gap between last observation of the

pup nursing and the next observation alone was greater than 12 days, the weaning date

was not considered accurate and the pup was not used in subsequent weaning date

summaries or analyses.

Analyses – I used Systat[®] version 11 (SYSTAT Software Inc., Richmond, California,

USA) for all analyses and a type-I error rate of 5% ($\alpha = 0.05$) in determining statistical

significance. I tested categorical variables for homogeneity of variance using a Bartlett's

test (Snedecor and Cochran 1967) and the distribution of continuous independent

variables for normality using Shapiro-Wilk test (Shapiro and Wilk 1965) prior to using

parametric statistical analyses. When noted, I applied transformations to correct non-

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[1] Maine Office of Geographic Information, Augusta, ME. http://megis.maine.gov/catalog/

normal distributions and all proportions were always normalized using an arcsine square-root transformation (Zar 1999).

Measurements including mass, girth, length, flipper length, and zygomatic arch that were obtained from pups that were classified as ≤1 dpp were used to estimate the characteristics of newborn pups. I tested for differences in birth characteristics between sexes and across years using a two-way ANOVA. For pups classified as nursing, I used the rate of change in measured characteristics from the first to second capture to estimate the rate of development during lactation. I calculated these rates as the difference between final and initial measurements divided by the number of days between captures. I considered the mass gain rates to be an index of fat accumulation since increases in bone and muscle mass are a much smaller contribution to the overall change in pup weight. The rate of change in standard length, therefore, is a better indicator of lean growth.

To explain the variation observed in mass gain rates during the lactation period, I used generalized linear models to examine the potential influence of year, Julian date (*i.e.,* day of year), mean age between capture and recapture, pup sex, pup initial standard length, female attendance, pup activity, and depth available on pup development. Standard length (*i.e.,* pup size) was included as a covariate since this measure may be correlated with the size and condition of the pup's mother (Ellis *et al.* 2000), which has been shown to account for a large portion of the variation seen in pup growth (Bowen *et al.* 2001*a*, Kovacs and Lavigne 1986). Female attendance (*ATD*) was calculated as the proportion of visual observations when the female was observed with the pup. The influence of pup activity was tested using two variables including, the proportion of VHF

relocations when the pup was found in the water versus hauled out (PIW) and the total movement distance divided by the number of days between capture and recapture (MOV). Depth available (DA) was the maximum depth found within the home range of each pup.

Only non-lanugo, nursing pups that were relocated 5 or more times during the period between capture and recapture were considered in this analysis. A quadratic effect of Julian date was included, but no other interactions were tested. Backwards stepwise model selection was used with an alpha of 0.05 to select the best factors explaining the variance in mass gain rate. The residuals of the global model were visually inspected and tested for normality (Looney and Gulledge 1985) and constant variance (Brown and Forsythe 1974).

Births were rarely observed and therefore could not be used to estimate the timing of births. Date of birth for individuals with an umbilicus was calculated by subtracting the estimated umbilical age of a pup from the capture date. An estimate of the mean date of pupping was obtained from the mean date of birth for all pups captured with an umbilical cord. Because of the increasing time spent monitoring and recapturing study animals throughout the season and a decline in the proportion of newborn observed relative to the entire pup population after mid-season, this method may produce a mean birth date estimate that is biased early. Two additional methods, that are more robust to the biases from a change in sampling effort, were used to estimate the pupping distribution. First, I used logistic regression to model the change in the probability that an umbilical cord was observed during each initial capture with increasing date. The effects of pup sex and year were also tested in the model. After removing non-significant

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parameters, I tested this model for lack of fit using the Hosmer-Lemeshow goodness of

fit test (Hosmer and Lemeshow 2000). The median effective date ($EL_{50} = -\beta_0 / \beta_{JulianDate}$)

represents the inflection in the distribution function and the point at which 50% of the

captures no longer have an umbilical cord. This corresponds to the time in the season

when the mean age of the pup population shifts from less than to greater than 6 days old.

The median date of birth, therefore, can be estimated by subtracting 6 days from the

median effective date.

It is likely that young pups were more frequently missed later in the season, since

they became a smaller portion of the total pup population. In a second method, I

attempted to account for these missed births by assigning ages to otherwise "unageable"

pups. I used a separate generalized linear model (GLM) to develop age predictions for

unageable pups captured each year since some measurements were not taken in 2004.

The ages of pups captured with an umbilicus were modeled against their sex, nursing

status, and morphometrics potentially providing indices of age during the lactation

period. Using Principal Components (PCA) analysis, I determined that there were two

major axes of variance in the morphometrics data. Based on inspection of the PCA

loading scores, girth and mean canine tooth lengths were found to best describe the two

significant components of variation in the data. The observed status of each pup was

included as a categorical variable in the model ("nursing" or "not nursing") since pups

with low mother attendance would be expected to grow less quickly. I constructed a

global model for each year consisting of all the chosen parameters and the likely

interactions. To validate this model, I used the log-likelihood ratio of this to the constant

only (*i.e.* null) model. The residuals of the global model were examined and tested for

normality (Looney and Gulledge 1985) and constant variance (Brown and Forsythe 1974) and if necessary the response variable was transformed to meet modeling assumptions. A set of candidate models were constructed from less parameterized subsets of the full model. A candidate model with the lowest Akaike Information Criterion for small sample size (AIC_c; Hurvich and Tsai 1989) was considered the best age prediction model (Burnham and Anderson 1998) and was used to generate ages for unageable pups. I back-calculated the date of birth for each pup and used the mean of the distribution for each year to estimate of the mean timing of births. I used a two-sample t-test to compare the mean timing of births and a two sample K-S test (Chakravarti *et al.* 1967) to test for a year effect in the distribution of births.

To estimate the duration of lactation, I used the mean weaning age of pups that were confirmed to be alone by continued absence of the female. Pups that were last seen with their mother at age 12 dpp or less were considered abandoned and not included in the mean estimate. Only a few individuals that were captured late in lactation were confirmed to be weaned based on observations. To estimate weaning morphometrics, I used non-nursing pups that were captured at ages older than the estimate of mean weaning age for the study population. The effects of pup sex and year on duration of lactation and weaning morphometrics were examined using a two-way ANOVA.

RESULTS

Sixty-six harbor seal pups were captured in 2004 and 89 pups in 2005 (Table 1.1). Those pups captured by hand on ledges (14.1 dpp) were older than could be captured using the dip net (6.4 dpp, two-sample t-test, $t_{stat} = 5.16$, $p < 0.01$). Overall, we were able to recapture 43% of the pup initially marked. Of the pups that received radios in 2004 (*n*

= 24), 66% were recaptured whereas 82% of the radioed individuals ($n = 45$) were

recaptured in 2005. Pups with a lanugo coat represented 6% of the captures in 2004 and

7% in 2005 (Table 1.1). Of pups less than 5 days old, those with lanugo ($n = 9$) were

lighter (9.5 kg) than those without (11.7 kg, $n = 66$, two sample t-test, $t_{stat} = 7.72$, p <

0.01).

Table 1.1. Summary of harbor seal pup captures in Maine during 2004 and 2005. Lanugo
pups were not included in the estimates of birth mass and mass gain rate.

Category	2004		2005		Total
	M	F	M	F	
Lanugo	2	2	4	2	10
Nonlanugo					
Not Recaptured	19	24	16	26	85
Recaptured	10	9	24	17	60
Total Pups Handled	**31**	**35**	**44**	**45**	**155**

The standard length of lanugo pups was 72.8 cm, which was also significantly

shorter than the average non-lanugo pup (two-sample t-test, $t_{stat} = 3.14$, p = 0.01). Of the

pups captured as newborns (≤1 dpp) those with lanugo were all male. These lanugo males

tended to be lighter than other newborn males, but the difference was not significant (9.8

kg vs.11.3 kg, two-sample t-test, $t_{stat} = 1.88$, p = 0.08).

Non-Lanugo Newborn Characteristics – Masses of ageable pups (*i.e.* 0-5 dpp) at the time of initial capture were positively associated with the assigned umbilical age category ($F_{1, 71}$ = 5.79, p = 0.02) after controlling for a significant size difference between males and females (ANCOVA, $F_{1, 71}$ = 5.91, p = 0.02). There was no significant difference in the sex ratio or number of newborns (≤1 dpp) captured each years (χ^2 = 0.31, *df* = 1, p = 0.58). The pooled estimate of birth mass was 11.1 (SE = 0.23) and among non-lanugo pups, males were slightly heavier than females but the difference was not significant (ANOVA, $F_{1, 20}$ = 0.34, p = 0.57). There was a significant year effect ($F_{1, 20}$ = 7.51, p = 0.01) with the average newborn weighing 10.5 kg (SE = 0.29) in 2004 and 11.6 kg (SE = 0.27) in 2005. Axillary girth did not vary among sexes (ANOVA, $F_{1, 20}$ = 0.70, p = 0.41) or between years (ANOVA, $F_{2, 20}$ = 0.47, p = 0.50). Newborn morphometrics are summarized in Table 1.2.

Standard length was also consistent between years (p = 0.98) and sexes (p = 0.37) but this measurement had considerable error depending on the degree of unruliness of the individual during handling. Zygomatic arch and right-rear flipper length were easier to obtain accurately during manual restraint of the animal, but these measures were only obtained in 2005. Males tended to have a larger cranial size (ANOVA, $F_{1, 10}$ = 4.60, p = 0.06) and longer rear flippers ($F_{1, 11}$ = 3.98, p = 0.07) than females, but these tendencies were non-significant; although the statistical power was low due to limited sample sizes. Of these two alternate measures of size, zygomatic arch was more highly correlated with standard length (Pearson's correlation, r = 0.44) than was rear flipper length (r = 0.04).

Table 1.2. Summary of the morphological characteristics of non-lanugo pups captured as newborns (≤1 day old). Means are shown with the standard error in parentheses. Sample sizes are provided in the column header if not specified above the sample mean.

Morphometric	Pooled Across Years		Pooled Across Sexes		Overall $n = 23$
	Males $n = 13$	**Females** $n = 10$	**2004** $n = 10$	**2005** $n = 13$	
Mass *(kg)* [a]	11.3 (0.36)	10.9 (0.25)	10.5 (0.29)	11.6 (0.27)	11.1 (0.23)
Axillary Girth *(cm)*	52.8 (0.88)	51.6 (0.94)	51.7 (1.19)	52.7 (0.69)	52.3 (0.64)
Standard Length *(cm)*	78.0 (0.97)	76.6 (1.20)	77.3 (0.96)	77.5 (1.15)	77.4 (0.76)
Zygomatic Arch *(cm)*	$n = 7$ 10.6 (0.09)	$n = 5$ 10.2 (0.18)	n/a	$n = 12$ 10.4 (0.37)	n/a
Right-rear Flipper Length *(cm)*	$n = 8$ 20.8 (0.34)	$n = 5$ 19.7 (0.34)	n/a	$n = 13$ 19.7 (0.28)	n/a

[a] ANOVA, Significant year effect.

Mass Gain Rate - During two years of research, 60 non-lanugo pups were captured at least twice in a season (Table 1.1). Due to a scale malfunction, mass gain rate was not available for one individual. Furthermore, 27 of these pups were not with their mother when recaptured based on observations or, in 2005, by inspection of blood for cloudiness. The mean rate of mass gain (*mGR*) for these unattended pups was 0.02 kg/d. Of fifteen non-nursing pups that were of known ages at the time of second capture (mean = 12.3 dpp, range: 2 – 30 dpp), 12 were 16 days old or less. Weaning normally occurs at between 15 and 31 dpp (Muelbert and Bowen 1993), therefore, pups were found unattended more frequently than expected. Thirty-two non-lanugo, attended pups gained mass at 0.45 kg/d (SE = 0.03, range: 0.09-0.79 kg/d) which was significantly higher than those that were unattended (two-sample t-test, t_{stat} = 6.59, p<0.01).

Factors Influencing Mass Gain – Thirty pups were included in the analysis of factors influencing mass gain rate since two pups had insufficient radio telemetry observation data (APPENDIX A, Table A.1). Transformations of the independent variables were required prior to running the backward model selection. Natural logarithm transformations were applied to the factors describing pup movement (MOV) and depth available (DA), pup attendance (ATD) was transformed to a categorical variable with values of 75% or greater being classified as 'high' and other values as 'low' attendance, and pup activity (PIW) was normalized using an arcsine square-root transformation. The results of the backward stepwise model selection revealed that there were significant within and between year effects, as well as, an affect of pup size and activity (PIW) on mass gain rate (r^2 = 0.60). The residuals for the selected model had constant variance and

were normally distributed ($r^2 = 0.99$). Nursing pups gained mass faster in 2004 than 2005 (GLM, $F_{1,24} = 5.51$, $p = 0.02$). There was a non-linear trend in mass gain rate during the pupping season with a significant effect of Julian date ($F_{1,24} = 11.7$, $p < 0.01$) and Julian date squared ($F_{1,24} = 12.1$, $p < 0.01$) in the model. Additionally, mass gain rate was positively associated with pup size ($F_{1,24} = 5.70$, $p = 0.03$) and activity in water (PIW; $F_{1,24} = 12.2$, $p < 0.01$). The coefficients of the backward stepwise selected model were:

$$mGR = -21.56 - 0.068(Year) + 0.286(Day) - 0.001(Day)^2 + 0.015(Size) + 0.400(PIW),$$

with year = '0' in 2004 and '1' in 2005.

Although not significant in the model, daily movement (MOV) was positively correlated with pup activity in the water (PIW; linear regression, $t_{stat} = 2.33$, $p = 0.03$). The method I used to determine if a pup was nursing differed between years, which may have potentially caused a between year difference in mass gain. In 2004 I used the observed presence of the mother, and in 2005 I used both female presence and blood lipemia to determine nursing. Thus, in 2005 there was an improved chance of incorporating pups in the analysis that had lower female attendance, since she didn't need to be observed for the pup to be considered nursing. I tested mass gain rate for a year effect using only pups that were observed with the female when recaptured. The year effect was still marginally significant (two-sample t-test, $t_{stat} = 1.87$, df = 25, $p = 0.07$). For this subset of data, the mean estimates of mass gain rate for each year were nearly the same (2004, mean = 0.56 kg/d and 2005, mean = 0.38 kg/d). Bad weather was also considered as a potential factor influencing pup development, since wind and waves may

cause female-pup separations (Boness *et al.* 1992) or limit the opportunities for the female to nurse her pup on shore. During 2005 there was a significant wind and rain event (*i.e.,* 'Nor-Easter') at the peak in the pupping season. When controlling for the significant within season birth timing effect on mass gain rate, 12 pups exposed to this major storm event gained mass at the same rate as pups measured during other parts of the season (ANCOVA, $F_{1,20} < 0.01$, $p = 0.99$) suggesting that this storm event was not responsible for the lower mass gain rates during 2005.

Lean Growth - Mostly as a result of measurement error, some pups had negative changes in standard length (*i.e.,* lean growth) between captures (range: -1.0 – 1.7 cm/d). Mean rate of growth was 0.26 cm/d (SE = 0.07) and was significantly greater than zero ($n = 57$, two-sample t-test, $t_{stat} = 3.74$, $p < 0.01$). Similar to mass gain, rate of growth for unattended pups was significantly lower than attended pups (two-sample t-test, $t_{stat} = 2.20$, $p = 0.03$). Pups that were with their mother at the time of recapture grew at 0.40 cm/d (SE = 0.10) compared to 0.10 cm/d (SE = 0.09) for pups that were unattended. There was no significant sex or year effect on growth (ANOVA, $p > 0.05$).

Timing of births – In 2004, the first pup found was discovered on the first day of searching (May 11th) and was estimated to be 3 days old. In 2005 we began ledge searches two weeks earlier and a 1 day old pup was observed on May 5th which suggests that the beginning of pupping was missed in 2004, however, only four pups were observed before May 11th in 2005 as a result of the earlier search effort. Based on umbilical aging, the earliest birth occurred on May 8th in 2004 and May 4th in 2005.

Searches were continued through July 1st in both years and no pups were observed with an umbilicus after June 1st in 2004 and June 4th in 2005. Using the distribution of pups captured with an umbilicus, the estimate of the mean date of birth was May 20th (SE = 0.50) in both years. There was no significant difference between years (two-sample t-test, t_{stat} = 0.55, p = 0.58). The logistic regression model adequately described the change in probability of observing a pup with an umbilicus with increasing date (Figure 1.2, McFadden's ρ^2 = 0.64, H-L$_{stat}$ = 10.54, df = 9, p = 0.31). Estimates of the mean and median dates of birth based on the presence of an umbilical cord and the logistic regression analysis are summarized in Table 1.3. Julian date was a highly significant parameter (t-ratio = 5.35, p <0.001) but there were no significant year (t-ratio = 0.56, p = 0.57) or sex effects (t-ratio = 1.23, p = 0.22). With non-significant parameters removed, the estimate of the median birth date was May 26th (Table 1.3, 95% C.I.: May 23 – May 28) using the following model coefficients:

$$ln\left(\frac{p_i}{1-p_i}\right) = -41.84 + 0.278(Julian\ date),$$

where p_i = probability of observing a pup without an umbilicus.

In subsequent analyses, ages were required for all pups including those that did not have an umbilicus when first captured. A separate GLM was used to predict age for each year and all candidate models are tabulated in Appendix B. In 2004, the residuals for the global model were found to be non-normal, so the response variable ('age') was

Table 1.3. Two estimates for the distribution of harbor seal pup births in Maine during 2004 and 2005 based on pups captured with an umbilicus and the median date in the modeled distribution of pups observed with and without an umbilicus with increasing date.

	2004	2005	Overall
Pups with an umbilicus			
Sample Size	32	43	2 yrs
Beginning of Search	May 11	Apr 28	
First Birth	May 8	May 4	
Last Birth	Jun 1	Jun 1	
Mean Date of Births	May 20	May 19	May 20
Median Date of Births	May 20	May 18	May 19
Standard Error	1.17	1.06	0.50
95% Confidence Limits	(May 16 - May 21)	(May 17 - May 21)	(May 17 - May 21)
Logistic Regression			
Sample Size	66	89	155
Median Date of Birth	May 26	May 25	May 26
Standard Error	2.41	1.61	1.05
95% Confidence Limits	(May 23 - May 30)	(May 22 - May 28)	(May 23 - May 28)
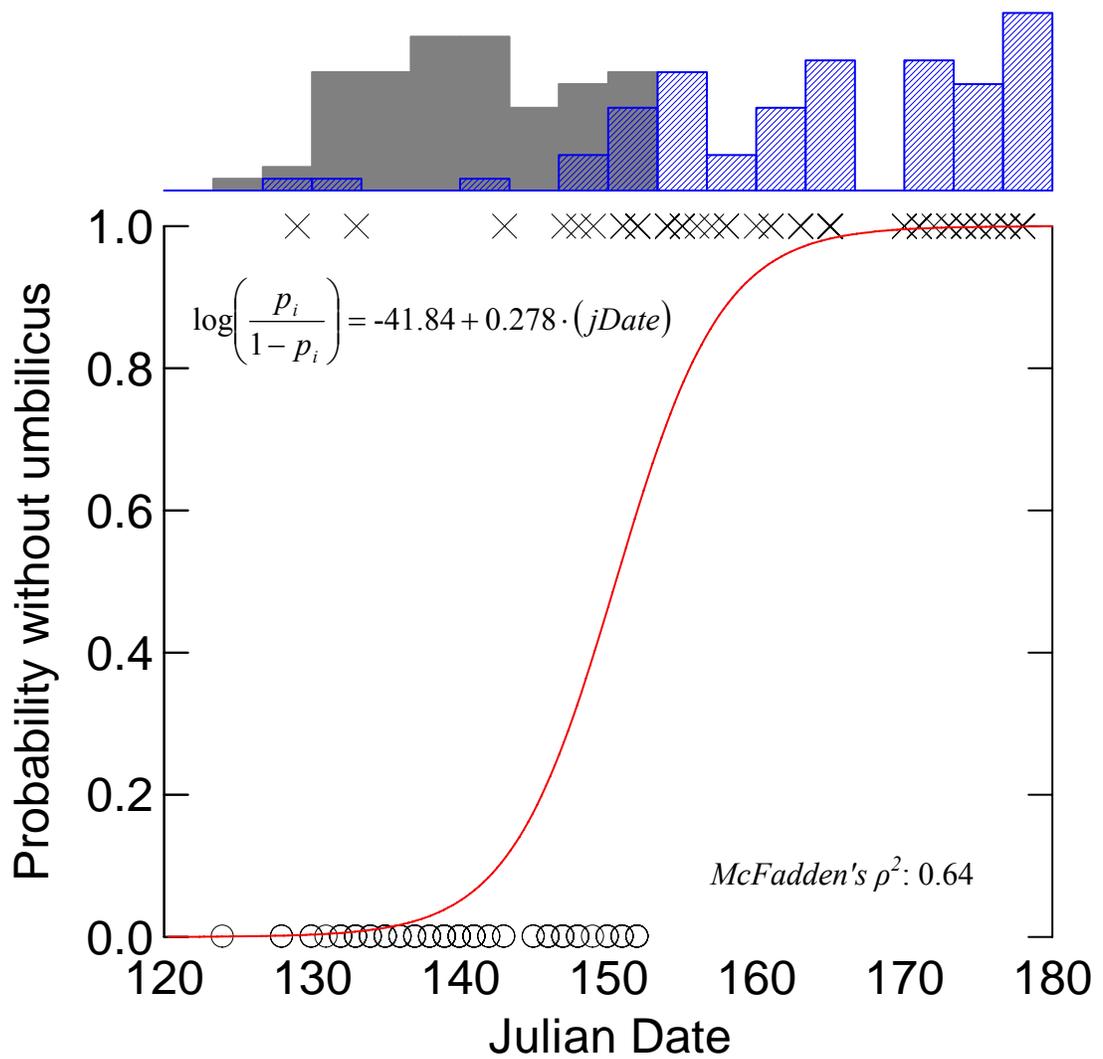
Figure 1.2. The logistic regression function curve describing an increasing probability of capturing a pup without an umbilicus with increasing Julian date. The frequency of pup captures with an umbilicus (circles) and without an umbilicus (x's) is shown at the bottom and top of the plot respectively. The histogram at the top of the figure shows the frequency distribution of pups captured with an umbilicus (solid) compared to those without (hashed), p_i = probability of observing a pup without an umbilicus.

transformed using natural logarithm. In 2005, the residuals of the global model were found to be normal and an untransformed response was used ($r^2 = 0.989$). The global model for each year was validated against the constant model. Model #15 was found to be the best candidate of the set for 2004 (Appendix B, Table B.1., AICc = -108.5, ($|\Delta AIC_c| > 2$). This model had an adequate fit ($R_{adj}^2 = 0.66$) with the following coefficients:

$$ln(age) = 0.862 + 0.041(axillary\ girth) - 0.439(nursing\ status),$$

with nursing status = '1', if nursing and '0', if not nursing.

For 2005, the top four candidate models were all similar in their ability to describe age ($\Delta AIC_c < 2$) but all of these models had parameters in common with the highest ranked and most parsimonious model (Appendix B, Table B.2., model #35). Measurements taken on the canine teeth in 2005 offered improvements in age predictions ($R_{adj}^2 = 0.86$) with the top model having the follow form:

$$age = -36.6 + 1.07(canine\ tooth\ length) + 0.85(axillary\ girth) - 7.92(nursing\ status)$$

These predictive models were used to assign ages to 79 non-lanugo pups that did not have an umbilicus at the time of initial capture. Date of births that were back-calculated using the age and capture date of each pup, were normally distributed in both years (SW, $P > 0.05$). The first year of the study was a 'leap' year. For the purpose of interpreting results, 2004 estimates were reported as they would appear in a standard

calendar year. Using this method, the estimated mean date of birth for all captured pups was May 24th in 2004 (Table 1.4, $n = 66$, SE = 1.12) and May 22nd in 2005 ($n = 89$, SE = 0.87). There was no significant difference in the mean birth date or the shape of the distribution between years (two sample t-test, $t_{stat} = 1.11$, p = 0.27, two sample K-S test, p = 0.51). For both years, the mean birth date was May 23rd (Julian Date = 143, SE = 0.50).

End of Lactation - The longest duration of nursing observed during this study was based on a female with her 37 day old pup. Twenty-six pups that were monitored until they were alone during two or more consecutive observations provided an estimate of 23.9 d (SE = 1.05) for mean weaning age. There was no significant difference in the weaning ages between years (ANOVA, $F_{1,22} = 0.56$, p = 0.46) or sexes ($F_{1,22} = 0.20$, p = 0.66). The heaviest female and male pups captured in two years were 26.8 kg and 28.0 kg respectively. For the purposes of estimating weaning traits, non-nursing pups that were captured older than 21.8 d (the lower 95% C.I. of weaning age) were considered weaned ($n = 47$). The average age of these pups was 29.4 dpp (range: 21 – 41 dpp) and their morphometrics are summarized in Table 1.5. There were no significant differences in weaning mass between years (ANOVA, $F_{1,43} = 0.39$, p = 0.53) or sexes ($F_{1,43} = 1.18$, p = 0.47) and the pooled estimate for weaning mass was 19.6 kg ($n = 47$, SE = 0.51). Weaned males had significantly longer rear flippers than did females (ANOVA, $F_{1,24} = 8.89$, p < 0.01), however, all other metrics did not vary between years or sexes (p > 0.05).

Table 1.4. Distribution of births for all pups captured in Maine during 2004 and 2005 after assigning ages to pups captured without an umbilicus ($n = 155$). Dates of births were back-calculated using the capture date and the umbilical age or GLM predicted age of each pup.

	2004	**2005**	**Overall**
Sample Size	66	89	2 yrs
First Birth	May 8	May 4	May 6
Last Birth	Jun 15	Jun 10	Jun 13
Duration of Pupping	39	38	38.5
Mean Date of Births	May 24	May 22	May 23
Median Date of Birth	May 25	May 23	May 24
Standard Error	1.12	0.87	0.50
95% Confidence Limits	(May 22 - May 26)	(May 21 - May 24)	(May 22 - May 24)

Table 1.5. Mean and standard error of the morphometrics for pups considered to be weaned based on being captured >22 days old and not nursing ($n = 47$). Flipper length, zygomatic arch, and canine length were not measured in 2004. Standard error is shown in parentheses and the sample sizes are provided in the column header if not specified above the sample mean.

Morphometric	Pooled Across Years		Pooled Across Sexes		Overall $n = 47$
	Males $n = 23$	**Females** $n = 24$	**2004** $n = 21$	**2005** $n = 26$	
Mass (kg)	20.4 (0.68)	18.8 (0.72)	19.1 (0.71)	20.0 (0.71)	19.6 (0.51)
Axillary Girth (cm)	69.1 (1.19)	67.9 (1.16)	67.2 (1.10)	69.5 (1.18)	68.5 (0.83)
Standard Length (cm)	89.8 (0.98)	88.5 (0.83)	88.8 (1.10)	89.4 (0.75)	89.1 (0.64)
Zygomatic Arch (cm)	$n = 13$ 11.1 (0.10)	$n = 13$ 10.9 (0.10)	n/a	$n = 26$ 11.0 (0.07)	n/a
Right-rear Flipper Length (cm) [a]	$n = 13$ 21.5 (0.20)	$n = 13$ 20.4 (0.28)	n/a	$n = 26$ 20.9 (0.20)	n/a

[a] ANOVA, Significant sex effect.

DISCUSSION

Six percent of the pups in this study had a lanugo coat when captured. This is similar to previous accounts for *P.v. concolor* with a 3-12% prevalence of lanugo observed in the St. Lawrence River Estuary (SLR, Dubé *et al.* 2003) and the 12.5% reported on Sable Island over a 10-year period (Ellis *et al.* 2000). My pooled estimate of birth mass for non-lanugo pups (mean = 11.1 kg) was similar to estimates reported in the SLR (11.1 kg, Dubé *et al.* 2003). Males on Sable Island weighed 11.4 kg while females weighed 10.9 kg (Bowen *et al.* 1994) compared to 11.3 kg and 10.9 kg estimated for each sex respectively in this study.

There was a large difference in mean birth masses between 2004 and 2005. Drastic yearly differences in pup birth mass have been previously shown on Sable Island with estimates increasing from 10.5 to 11.5 kg between two years (Bowen *et al.* 1994). This change on Sable Island may have been attributed to a shift in the pup sex ratio in favor of males which were significantly heavier at birth. In the current study, males also tended to be heavier than females but the sex ratios of captured newborn pups during the two years were similar and therefore could not account for the significantly higher birth mass seen in 2005. At birth, male harbor seal pups are approximately 4% heavier than females (Ellis *et al.* 2000). In previous studies this difference was not significant unless sample sizes were large (*n* = 375, Ellis *et al.* 2000) or size variation due to the influence of maternal mass was controlled (ANCOVA, Bowen *et al.* 1994). In this study, males at birth tended to have longer flippers than females, with this difference becoming significant at the time of weaning.

Biologically, mass dimorphism is likely less important to the harbor seal than it is

for larger, colonial breeding phocids. For example, gray seals compete with other males

to maintain control of their harems in a colony – with the number of females in their

harem determining their reproductive success. Male harbor seals may maintain lekking

territories during the breeding season, which requires the male to defend an area from

other males to ensure mating opportunities (Boness, D.J., pers. comm.). In this case larger

size may actually hinder a male when challenged since the tactics used to fight in water

probably rely on speed and agility (Le Boeuf 1991). Longer rear flippers presumably

provide better propulsion and maneuverability in the water. This form of sexual

dimorphism could be established and maintained if males with longer flippers are

experiencing better reproductive success.

Pup Development during Lactation – My estimate of mass gain rate (0.45 kg/d) is lower

than previously reported values for this subspecies. Other estimates have ranged from

0.54 in the SLR (Dubé *et al.* 2003) to 0.7 kg/d on Sable Island (Bowen *et al.* 2001*a*). My

estimate, however, is not outside of the range seen for this species in other parts of the

world. In British Columbia, pups (*P.v. richardsi*) gained weight at 0.39 kg/d (Cottrell *et

al.* 2002) and a value of 0.36 kg/d was reported for pups of the harbor seal (*P.v. vitulina*)

in England (Vaughan 1978). Other species including the gray seal and Southern elephant

seal have shown up to a two-fold difference in the mean mass gain across populations

(Bowen 1991). Minimum and maximum values represent the extremes that a population

can support under the given constraints of local conditions. On Sable Island, between

1989 and 1996, the range of mass gain rates observed was 0.3 - 1.1 kg/d whereas mass

gain ranged from 0.118 to 0.875 kg/d in the SLR between 2000 and 2002. Consistent with having a higher mean value, the extreme values of mass gain rate in both of these areas were higher than those observed in Maine (range: 0.09 - 0.79 kg/d).

The mean rate of pup development during lactation is influenced by the age structure of a seal population, the general postpartum condition of females and the resources and the habitat available in the vicinity of the pupping area. In this study we were unable to capture and collect data on parturient females; however, population-wide generalizations can be made based on the differences between Maine and Canadian populations. Limited population trend data for northeastern Canada suggests that these pupping aggregations are likely to be stable or experiencing a slight decline. On Sable Island, there has been a drastic decrease in the number of females and pup production over the past decade. In contrast, the Gulf of Maine population has continued to increase. In a growing population, younger animals represent a larger portion of the female cohort than they would in a stable or declining population. Thus, potential differences in the age demographics might explain the lower mean mass gain rates observed, but does not adequately explain the lower range of values unless older females are absent and younger females are giving birth in the Maine population.

There were significant between- and within-season temporal affects on pup mass gain rates. Mass gain rates were significantly higher in 2004 and near the middle of the pupping season. Across and within season variations in harbor seal pup mass gains have been previously shown (Bowen *et al.* 2003, Ellis *et al.* 2000). On Sable Island, growth was positively influenced by parturition date (Ellis *et al.* 2000), since larger females give birth later in the season (Bowen *et al.* 2001*a*). In this study, the effect of Julian day was

non-linear and significant after controlling for pup size, which serves as an index of female size and condition. These results suggest that there was a decline in pup mass gain near the end of the pupping season unassociated with female size and condition.

Because breeding occurs near the end of the pupping season, females that nurse their pups late in the pupping season may become increasingly interrupted by males during this time. Alternatively, changes in resources may influence pup growth, since females increasingly rely on local resources to provision their pup late in lactation. In larger pupping aggregations, such as in Maine, females may increasingly deplete the local prey base during the pupping season. Low resource availability is coupled with additional costs to females as they travel to more suitable foraging areas. Resource limitations could explain an apparent decline in mass gain rates late in the pupping season, as well as, the overall lower mass gain rate for this population.

Habitat type and disturbance influence the activity levels of harbor seal pups and therefore, could negatively influence mass gain. At one extreme, the pups on Sable Island have access to beaches during all tides and are rarely disturbed by human activity. Pups at this location were found to spend about 39% of their time on land (Bowen *et al.* 1999). In contrast, the majority of substrate used for hauling out in Maine is either intertidal or extremely rocky and difficult to access during lower tides. Additionally, the harbor seals at this location are skittish and entire pupping ledges are occasionally emptied on the approached of recreational boat traffic (although surprisingly unaffected by nearby lobster boats). Results from time-depth recorder data (Chapter 2) suggested that pups spent on average 61% of their time in the water during this study. I would expect that active pups would have a higher metabolic demand and possibly fewer opportunities to

nurse, but a positive association between activity levels (PIW) and mass gain rates presented here suggests that this is not the case. Disturbance probably does not explain differences in mass gain rates between this and other populations.

For a nursing pup, fat deposition measures the amount of energy intake after accounting for metabolism. If equally provisioned, active pups would be expected to develop more slowly than those that are relatively sedentary. In this study, pups that were more active (PIW) were associated with having higher mass gain rates. Increased pup activity does not mechanistically explain increased growth but these two factors may be linked through an intermediary factor. Pup mass gain rate and activity level may be correlated with female size and condition. A larger female would have more reserves to provision her pup and may be able to invest more time during lactation actively swimming with her pup rather than foraging. This would result in a positive association between these two factors. Alternatively, faster growing pups may be less lethargic and surplus energy may affect their willingness to explore the area around their haul outs with or without their mother. Based on time-depth recorder data, the proportion of time that pups were in water and their mean diving depth was positively correlated with mass gain (Chapter 2). These independent associations between mass gain and pup behavior further suggest that females (through their attendance) are playing a part in motivating their pups to enter the water and follow.

Within my study population, mass gain rates were not significantly correlated with the depth available in the vicinity of the pupping ledges used by female-pup pairs, the amount of movement that the female-pup pairs exhibited, or the amount of observed female attendance. Depth available was intended to provide an index of pupping site

quality based on allowing the female to access to deep benthic prey and reduce her commuting costs. Females have been shown to travel up to 45 km from natal sites late in lactation (Thompson *et al.* 1994). Within a distance of 13 km of all pup home ranges in this study, water as deep as 100 m was available to all females. Depths within 2 km of a pup's home range, therefore, may not be a sensitive index of site quality or play an important role in influencing the quality or quantity of pup provisioning.

Females may exhibit diurnal foraging cycles. Because relocation data in this study was restricted to daylight hours only, my estimates of attendance (ATD) may have not provided an accurate index of female attendance. Although pup movement rates varied by two orders of magnitude (range: 32 – 3088 m/d), this had no apparent effect on pup mass gain rates. In some cases, the cost of moving a pup between haul-out sites may be offset by increased female foraging opportunity and increased pup attendance when she hauls out. Alternatively, the energetic cost of swimming may be insignificant compared to the energy provided during normal nursing bouts. This may also explain why increased time spent in water (PIW) did not negatively affect mass gain rates. Although daily movement (MOV) was not a significant factor influencing mass gain rate, it was positively correlated with in-water activity. Females may employ different strategies in caring for their pup depending on their size and condition. Small females may leave their smaller and less capable pup behind at haul out sites while larger females may move their pups more freely between ledges. Based on the large variation in pup activity and movement observed in this study (Appendix A), most females are probably employing a lactation strategy intermediate to these two hypothetical extremes.

The estimated weaning mass of 19.6 kg in this study was lower than the mean

reported for pups on Sable Island (24.8 kg, Bowen *et al.* 2001*a*). Nursing pups achieve

their greatest mass on the day of weaning after which they lose weight for several weeks

before achieving a net positive energy balance (Muelbert and Bowen 2003). In this study,

it was not feasible to capture pups on their estimated weaning date. The capture data used

in my estimates were likely from pups weaned sometime before or after the time of

capture; therefore, mean weaning mass was likely underestimated. The range of weaning

masses was also lower in this study, with the largest capture weight for a pup being 28

kg. This is considerably smaller than the 34.5 kg maximum reported on Sable Island

(Bowen et al. 2001*a*). Additionally, in the SLR, pups over 30 kg were commonly

captured (Schreer, J.F., pers. com). This suggests that pups in Maine were generally

lighter at weaning consistent with the lower range of mass gain rates observed.

Timing of Births – Prior to this study, there were only anecdotal estimates of the timing of

harbor seal pupping in Maine. Earliest accounts suggested that pupping occurred from

late March to early June (Allen 1942, Hunt 1948). Later estimates acquired through

personal communications with biologists (Bigg 1969*a*) established that births occurred

from late April through mid-June. Most recently, newborns were observed after April

28th (Gilbert, pers. comm.). In this study I estimated the timing of births using three

methods. Using only the observed distribution of pups with an umbilical cord provided an

estimate that was likely to be biased earlier than the true mean date of births. During both

capture seasons we placed an increased emphasis on recapturing tagged animals late in

the season. This likely reduced the potential of observing and capturing younger pups late

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in the season. At the same time, younger pups continued to represent a smaller proportion

of the population and thus were more difficult to identify. Therefore, we likely missed

observations of births at the end of the pupping season. This potential bias is apparent

from the abrupt change from regularly observing newborn pups to none observed after

June 1st (Figure 1.2). The logistic regression model was likely more robust to the under-

representation of newborns in the sampling distribution late in the season. This method

incorporates the tendencies of the population throughout the season when estimating the

probability function. As a result, the logit function represents a more normalized

transition from ageable to unageable pups and extends the otherwise truncated tail in the

sampled newborn distribution. Of course, if an extremely large portion of the late season

births were not observed, this method would produce an estimate that is also biased

earlier than the true mean.

To overcome this potential bias stemming from missed births, I used a third

method to determine the mean date of parturition. This method used the mean age of

births for all pups that were captured and does not require that pups are captured within

the short interval of time while they still have their umbilical cords. As a result, the

estimate of the end of the birth timing is not restricted by the sampled age distribution.

Additionally, sampling the pup cohort beyond the midpoint in the birth distribution

serves to further refine the estimate of the mean date of parturition. As a result, the last

births were found to occur 15 and 10 days later than predicted by using ageable pups

alone in 2004 and 2005 respectively (Table 1.4). Most of the pups captured late in the

season were not ageable ($n = 80$) and were given a predicted age based on morphometrics

and nursing status. Prediction bias was not a concern since the aging models had

adequate fit and the residuals were normally distributed. The validity of the estimate of

the timing of births is not contingent on the precision of age estimates, as long as those

estimates are not biased. This is because the prediction errors from the model (with a

mean of zero) would tend to cancel out, since only the mean of these values were used to

estimate the pupping date. The mean date of births as estimated from all pup captures was

May 23rd (Table 1.4). This estimate was later than estimates inferred from the distribution

of ageable pups yet earlier than predicted by the logistic regression model.

Previous estimates of the timing of births on Sable Island (44.93º N, 60.00º W),

which is located at approximately the same latitude as Maine, were consistent with those

observed in this study. In 1970 – 1973, the median date of birth was determined to be

May 26 (SE = 2, n = 3) from the midpoint in the distribution of observed births (Boulva

1975). Surveys from 1987 to 1991 suggested a mean parturition date of May 22 (SE =

0.3). During a population decline on Sable Island, however, parturition dates occurred

later; possibly in response to the associated changes in population age structure. During

the period between 1992 and 1996 the mean date of pupping occurred on May 28th (SE =

0.3) and from the individual year estimates provided in Bowen $et~al.$ (2003), this date is

significantly later than the date observed in this study (two-sample t-test, t_{stat} = 3.17, df =

8, p = 0.01). Farther to the north in the SLR, a recent account of the timing of pupping

reported a mean estimate of 26 May (SE = 1.6, Dubé $et~al.$ 2003). Although this value is

later than the estimate in this study, the difference is not significant (two-sample t-test,

t_{stat} = 1.64, df = 3, p = 0.19).

Influence of Photoperiod on Birth Timing - Photoperiod is the proximate cue for delayed implantation. If individuals of a population respond to the same critical day length, births are expected to occur later with increasing latitude. According to the empirical model originally developed by Tempte *et al.* (1991) and later corrected (Dubé *et al.* 2003):

$$Pupping\ Day = 82 + 1.69(latitude)$$

the mean pupping date for my study area would be May 27th. This prediction is 4 days later than the mean pupping date observed in this study. This discrepancy is reasonable given that no formal estimate was available to the authors at the time of the analysis and June 1st was used as an estimate for the timing of births in Maine when developing this latitudinal birth clines model.

To my knowledge, clines in pupping as a result of latitudinal changes in photoperiod have not been discussed using a theoretical approach. If photoperiod was the only factor driving the parturition dates across latitudinal gradients, temporal differences in birthing across pupping areas should be predicted by differences in day length experienced by individuals of those localities. Embryonic implantation has been previously estimated to occur at between 260-270 days pre-partum in the harbor seal (Fisher 1954, Bishop 1968, Bigg 1969*b*). Based on the range of mean parturition dates published for *P.v. concolor* (May 20th to June 1st, Bowen *et al.* 2003) implantation is likely occurring sometime between August 15th and September 15th. Within this range of potential implantation dates the maximum difference in day length between populations would be experienced at the earliest date. On August 15th, the day length in the SLR is

14.35 hrs and 14.02 hrs in Maine; with the difference being 0.33 hrs (20 minutes; Keisling 1982). With day length changing at a rate of 0.052 hrs/d in the northern population, once the critical day length is reached in the south there would be an approximate 6 day lag before this critical day length would be experienced in the north. If, however, the critical day length occurs closer to September 15th, then the predicted lag in implantation would be only around 1 day. Because population condition and age structure influence mean pupping date, this value is not necessarily comparable between pupping areas. However, if births in different populations are influenced by the same host of factors, then the range of values should be comparable. The earliest births in Maine occurred around May 6th while the SLR population saw the first births about 7 days later on May 13th. Similarly, the mean last birth in the SLR occurred on June 18 (5 days later than in Maine population). This lag in birth timing is consistent with expectations if day length was the dominant factor establishing the timing of births in these populations. Day lengths experienced by these two populations become increasingly similar on the approach of September 21st (Autumnal equinox) when both populations would experience a 12 hour day. These results suggest that embryonic implantation may be occurring in late August or early September, rather than late September as proposed by Dubé *et al.* (2003).

The duration of birthing in this study is similar to the 37 day birthing period reported for the SLR. In contrast, the mean duration of birthing on Sable Island during 1992 – 1999 was 26 days (Bowen *et al.* 2003). This shorter pupping period compared to Maine was caused by a later beginning of births (18 May) since the mean ending of births, 12 June, was similar to the results of this study. This difference in the beginning of

births is likely attributed to the difference in population status between Maine and Sable Island. Younger females, that generally have pups earlier in the season, have become increasingly absent at the Sable Island pupping site. In earlier studies of this population, early newborns were regularly observed around May 8th and the last births occurred on June 9th; a duration of 33 days (Boulva and McLaren 1979). Females that move southward prior to implantation would tend to extend the left tail in the birthing distribution. The higher degree of pupping synchronicity seen on Sable Island in more recent years could also be attributed to a more restricted range or a different timing in seasonal movements compared to the mainland aggregations.

The genetic relatedness of populations in the Gulf of Maine to those at the northern extent of the range is currently unknown. Evidence from tagging studies suggests that there is some mixing between the Sable Island population and those in the south during the non-breeding season (Baird 2001). Given the long range movement and dispersal capability of the species, we might expect genetic continuity throughout the range of *P.v. concolor*; however, genetic sub-structuring can be established if there is some degree of isolation between breeding populations and site fidelity. In Europe, populations of *P.v. vitulina* along the coastline of the North Sea were found to be lacking in genetic diversity (Swart *et al.* 1996) while populations on the West coast of Scotland and in Iceland on the outer edge of the range were genetically differentiated from each other and the North Sea populations (Stanley *et al.* 1996). Goodman (1998) concluded that distances of 300-500 km produced genetic structuring in *P.v. vitulina* as a result of population separation by open water and discontinuity in coastal breeding locations. Analysis of microsatellite and mitochondrial marker data from Hudson Bay, Miquelon,

and Sable Island found three genetically distinct populations when included with data for all of the Northern Atlantic (Coltman *et al.* 2002). More recent fine scale analysis of 9 populations of *P.v. concolor* confirmed the initial findings and there appear to be at least 3 distinct groups at the northern end of the range, including Hudson Bay, Sable Island, and sites connected along the Eastern Canada coastline from Labrador to Nova Scotia (Dorothee *et al.* 2005). Genetic differentiation between the mainland group and the Sable Island population, which is only 180 km off the coast of Nova Scotia, emphasizes the degree to which open water can segregate breeding populations. Genetic structuring, however, may also potentially occur along stretches of continuous coastline if pupping habitat is sufficiently discontinuous. The Pacific harbor seal is genetically divided into two or more subpopulations from Mexico to Alaska (Burg *et al.* 1999, Lamont *et al.* 1996). Mitochondrial analysis of harbor seals along the coastline of Alaska revealed that sub-structuring, influenced by female breeding site fidelity, was occurring within the range of 150 to 540 km, but varied by region (O'Corry-Crowe *et al.* 2003). Because *P.v concolor* pupping areas at the southern end of the range are potentially separated by open waters of the Bay of Fundy and this subspecies has recently recovered from low densities; it is possible that the Gulf of Maine population is genetically differentiated.

Conclusions – The timing of births and mean mass gain rates for harbor seal pups in Maine is not inconsistent with my expectations based on estimates reported for the SLR and Sable Island. Relative to the SLR, the pupping dates observed in this study can be explained by latitudinal differences. Although lower than reported in previous studies, a lower mean mass gain in Maine was expected, based on differences in population status.

The observed lower range of mass gain rates and weaning masses, however, are not explained by differences in population age structure. Behavioral plasticity in maternal investment strategies or reduced resources near Maine pupping sites are potential explanations for these results; although resource limitations may also explain the decreasing trend in mass gain rates late in the pupping season. Surprisingly, increased pup activity in this study was associated with higher mass gain rates. This is most likely attributed to the influence of the female on pup behavior, since larger females are capable of investing more in pup rearing in terms of milk provisioning and attendance. Further investigation of pup developmental characteristics coupled with information about the size and condition of parturient females in Maine would be necessary to better interpret these findings. Furthermore, between population differences in pupping characteristics that I've presented here ignores any potential effects due to genetic sub-structuring. An examination of the genetic relatedness between the Gulf of Maine population and northern Canadian populations is warranted given that genetic sub-structuring is known to occur in the harbor seal over short distances.

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CHAPTER 2

ONTOGENY OF HARBOR SEAL (*PHOCA VITULINA*) PUP DIVING BEHAVIOR IN

RELATION TO ENVIRONMENTAL AND MORPHOLOGICAL FACTORS

INTRODUCTION

Maternal investment strategies differ among species, as females attempt to

maximize fitness under the constraints of their environment (McFarland 1993). Within,

Phocidae, the duration of pup care is relatively short (Oftedal *et al.* 1987) and pups are

generally sedentary for the entire nursing period (Bowen 1991). During a subsequent

post-weaning fast, pups must have sufficient reserves until they develop into independent

foragers. Pup survival, therefore, is heavily influenced by the amount of milk

provisioning offered by the female (Harding *et al.* 2005, Hall *et al.* 2001, Millar 1977).

Pups of the Weddell seal (*Leptonychotes weddellii*), bearded seal (*Erignathus barbatus*),

ringed seal (*Pusa hispida*), and harbor seal (*Phoca vitulina*, Linnaeus 1758) remain

relatively active and dive with the female during the lactation period (Bowen 1991). This

strategy likely evolved to cope with the birthing substrate and predation pressure

experienced by these species in their pup rearing environments. Because the female

interacts with her pup, milk provisioning may not be the only form of maternal

investment influencing pup survival in these species since pups learn about their

environment and develop skills from this interaction.

The harbor seal gives birth to the most precocial pup among phocids seals

(Bowen 1991). Pups are born with traits that likely evolved in response to an early

aquatic life style, including an insulating, subcutaneous fat layer and a hydrodynamic

adult pelage (Bigg 1981, Oftedal *et al.* 1991). Through the encouragement of the female,

harbor seal pups will enter the water within minutes of birth (Newby 1973) and continue

to spend around 50% of their time in the water during the 24 day lactation period (Reder

et al. 2003, Muelbert and Bowen 1993). The amount of time pups spend in water tends to

increase with age and during high tides (Jorgensen *et al.* 2001). This highly aquatic

behavior is believed to have evolved in response to the limitations in the suitable

substrate available for birthing in more temperate regions (Renouf *et al.* 1983, Lydersen

and Kovacs 1999). Unlike phocids with inactive young, female harbor seals are free to

give birth on islands and ledges which become submerged during the high tide and can,

therefore, avoid large islands and coastal beaches accessible by terrestrial predators

(Bowen 1991).

In the first week following birth, females encourage their pups to dive and follow

them (Venables and Venables 1954). During this period, a female must forgo efforts to

forage as she limits her depth and dive duration in accommodating the limited diving

ability of her pup (Bowen *et al.* 1999). But as a small-bodied phocid, the demands of

lactation are extremely high since females lose 33% of their mass and 79% of their fat

reserves during the first 19 days of lactation (Bowen *et al.* 1992). Thus, females are

forced to begin foraging by mid-lactation (Boness *et al.* 1994, Thompson *et al.* 1994) and

must make a choice whether to bring or leave their pup. The swimming ability of the pup

may dictate whether it is encouraged to follow or left behind at the onset of foraging. For

a smaller female that must begin foraging earlier in lactation (Boness *et al.* 1994) the pup

is more likely to be left since it is a less capable swimmer. As the pup becomes more

developed, however, the female may choose to have her pup accompany her on foraging

bouts or it may begin to follow unsolicited. Increased pup mobility may aid the female in

reestablishing a positive energy balance by allowing her to relocate to better foraging

areas and reduce the energetic costs otherwise associated with commuting back to the

natal haul out site to nurse. The pup may also benefit by staying with the female as she

begins to forage because missed nursing opportunities may reduce overall weight gain of

the pup. Remaining with the mother in the foraging areas could maximize milk

consumption, as the pup might capitalize on opportunities to nurse whenever the female

hauls out to rest. Additionally, with presumably more time to access prey, the female

should be able to increase the quality as well as the quantity of milk being provided to the

pup during each nursing event.

If the female does not haul out during foraging bouts, accompanying the female

would offer no energetic benefit to the pup. Increased activity during these bouts would

then tend to consume the pup's fat reserves. Remaining active during the provisioning

period may benefit the pup indirectly, however, by offering improved diving skills, a

more developed physiological dive response, and experience. As harbor seals rely to

some degree on benthic prey (Payne and Selzer 1989) a large proportion of dives by adult

harbor seals are to the ocean floor (Tollit *et al.* 1998). To optimize foraging efficiency

they are motivated to maximize 'bottom time' which is the period of time spent at the

bottom of a dive searching for food (Ydenberg and Clark 1989, Horning and Trillmich,

1997). Although pups generally do not attempt to feed themselves until weaning

(Muelbert and Bowen 1993, Muelbert *et al.* 2003), a pup with its mother during foraging

might become a more proficient diver. Additionally, by observing the female the pup

would likely gain valuable experience about how and where to forage (Costa 2001). The

combined contribution of diving and foraging experience may have a significant effect on survival if it allows the pup to more quickly achieve nutritional independence after weaning.

Despite its extremely aquatic behavior from birth, the physiological dive ability of a harbor seal pup is limited throughout lactation. In all mammals, the ability to dive is ultimately constrained by the amount of oxygen available to maintain brain function during breath holding (Kooyman 1989). During a dive, oxygen is consumed by basal metabolic function and muscle activity. The length of time a dive can persist, therefore, is a function of the total body oxygen stores (TBO) and the rate at which the oxygen is consumed; also called dive metabolism (Lavigne *et al.* 1986, Ponganis *et al.* 1993). Because TBO increases linearly with mass and metabolism increases at a rate of mass to the 0.75 power (Kleiber 1961), pups have higher mass specific oxygen consumption rates and therefore limited dive ability compared to adult seals. During the nursing period pups also have lower mass-specific TBO relative to adults. This is in small part due to reduced mass specific blood oxygen stores but, is largely due to a limited muscle myoglobin concentration compared to adults (Jorgensen *et al.* 2001, Burns *et al.* 2005, Clark *et al.* in review). Newborn pups also need time to develop certain adaptations that marine mammals have evolved to extend dive time through minimizing oxygen consumption during breath holds (Butler and Jones 1997). These adaptations, which include reduction and stabilization of diving heart rate (Lapierre *et al.* 2004, Greaves *et al.* 2005), control of pre- and post-dive respiration (Lapierre *et al.* 2004), reduction in thermal output (Hansen and Lavigne 1997) and vasoconstriction (Cherepanova *et al.* 1993), are not developed at birth but continue to develop with age.

Like any behavior, diving is the net expression of motivators and constraints operating on an individual at a given time. Adult seals are motivated to remain under water for various reasons, including to forage, avoid predators, avoid extreme surface conditions, travel, and to socialize (Lydersen and Kovacs 1999). For pups, diving is mostly out of interest in maintaining contact with their mother (Bowen *et al.* 1999, Renouf *et al.* 1983) but their motivation is similar; maximize submergence time while minimizing the interval at the surface necessary for respiring (i.e. 'post-dive surface interval'). Seals do not maximize underwater activity by maximizing individual dive duration because there is an abrupt change in the relationship between the post-dive surface interval necessary to ventilate and the increased dive duration. This change occurs when an animal exceeds its aerobic dive limit (ADL). This limit is defined as longest dive an individual can sustain without experiencing an increase in post-dive lactate levels (Kooyman *et al.* 1983). After this limit is reached, there is a sharp increase in the time spent ventilating with increased dive duration and dive efficiency declines (Kooyman *et al.* 1983). The majority of neonate harbor seal pup dives have been reported to be less than their estimated ADL (Boness *et al.* 1999, Jorgensen *et al.* 2001). These comparisons between dive behavior and calculated ADL have used individual based estimates of TBO but estimated dive metabolism using a theoretical approach since dive metabolism is difficult to measure in the field. These previous findings, therefore, fail to acknowledge that neonate dive metabolism may be extremely high during the first week post-partum due to inefficient diving and swimming.

Measured changes in dive duration of nursing harbor seal pups may be most pronounced in the first 10 days post-partum (dpp) before females begins to forage

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(Bekkby and Bjorge 2000, Boness *et al*. 1994). This dramatic increase in dive

performance was shown to not be entirely explained by increases in TBO (Jorgensen *et*

al. 2001) as blood and muscle oxygen stores increase only slightly from birth to weaning

(Burns *et al.* 2005, Clark *et al.* in review). Changes in dive metabolism may better

explain early increases in dive durations since the apnoeic heart rate dive response was

shown to develop in the first week after birth (Lapierre *et al.* 2004, Greaves *et al.* 2005).

Early changes in performance may also be associated with behavioral learning and the

physiological training effect which would serve to reduce the energetic costs associated

with dives. Newborns tend to 'dog paddle' initially before learning to use their rear

flippers for propulsion sometime during the first few days (personal observation). Higher

efficiency stroke and glide techniques used for propulsion by marine mammals probably

improves with increased practice (Williams *et al.* 2000). Early dive efforts may also be

impeded by improper breathing since pups may not initially know how to hyperventilate

and partially evacuate their lungs prior to diving (Kooyman *et al.* 1989, Butler and Jones

1997). Through trial and error, coordination and breathing strategies likely develop

within the first few days and along with physiological training may in part explain the

marked changes in pup dive performance early in lactation.

Similar to dive duration, maximum swimming speed tends to increase with age

during lactation although average daily swimming speeds are constant (Jorgensen *et al.*

2001). An important measure of dive performance that is related to swimming speed is

the rate at which an animal can ascend and descend in the water column. In situations

when a dive is nearly vertical, this metric is equivalent to swimming speed modified by

buoyancy. If the physiological effects of pressure are ignored, the maximum dive depth

that an individual can attain is limited by the maximum length of time an animal can breath-hold while transiting vertically in the water column at the most efficient speed (Butler and Jones 1997). Maximum depths attained by pups, however, are generally much shallower than their potential dive ability. This is likely because the bathymetry in the vicinity of the natal haul-out site is shallow and therefore constrains pup diving behavior (Bekkby and Bjorge 2000, Greaves *et al.* 2005).

Since the ability to dive is fundamental to seal foraging ecology, there is likely to be strong selection for capable, efficient divers (McCafferty *et al.* 1998). This may be especially true for neonate harbor seals during the transition from nursing to independence. During the limited time of maternal care, harbor seal pups potentially benefit from developing the skills necessary to become self-sufficient. For newly weaned pups, the ability to dive deep is important since less maneuverable prey such as amphipods and crustaceans are more commonly found in the benthos. Thus, experience diving during the lactation period could directly influence the ability of the pup to provision itself after weaning.

Differences in reported pup diving performance between studies, suggest that bathymetry may play an important role in pup diving behavior. The varied ocean topography in the vicinity of natal haul-out sites around Deer Isle, Maine, offers an opportunity to test this hypothesis. In this study, I will attempt to explain differences in activity and dive behavior of nursing harbor seal pup using age, indices of physiological dive ability (e.g. mass gain rate and birth mass), tide states, and mean and maximum bathymetry available in the vicinity of natal haul-out sites.

STUDY AREA

This research was conducted in the vicinity of Deer Isle, Maine (44° 09.28' N, 068° 39.91' W). This area is comprised of many islands and intertidal ledges well suited for harbor seal pupping. The north and eastern boundaries of the study area were marked by Crow Island and Egg Rock to the north and Marshall Island at the southeastern end of Jericho Bay. The western boundary was defined by West Mark Island Ledge near Stonington, The Brown Cow, and Scraggy Ledge along the eastern edge of Penobscot Bay (Figure 2.1, Figure 2.2). Bathymetry within this 110 km^2 area is varied with a mean depth of 11.6 m and several channels reaching 62 m deep. The sea floor continues to fall in the surrounding 5 km where the mean depth is 16 m and the sea floor reaches 105 m.

MATERIALS AND METHODS

Pup Handling and Data Collection - Harbor seal pups were captured on or near ledges throughout the study area (Figure 2.2) between May 12th and Jun 30th of 2004 and 2005 by hand or using a long pole dip net (see 'Materials and Methods', Chapter 1). Thirty-eight pups were sexed, weighed to the nearest 0.2kg and assigned an age based on the condition of the umbilicus (Boulva 1975) or using an age prediction model when the umbilicus was not present (Chapter 1). In 2005, 12mL of blood serum was obtained from the extra dural vein using a *Vacutainer*® *System* (Becton, Dickinson and Co., Rutherford, U.S.A.) with a 2.5-inch, 18-gauge needle. Blood serum was later examined for cloudiness; an indicator of nursing (Bowen *et al.* 1985). A head-mounted VHF radio transmitter (RMMT-4, Lotek Wireless Inc., St. John's, Newfoundland, CANADA) and a time-depth recorder (TDR) assembly were attached to each pup's fur (Fedak *et al.* 1983)
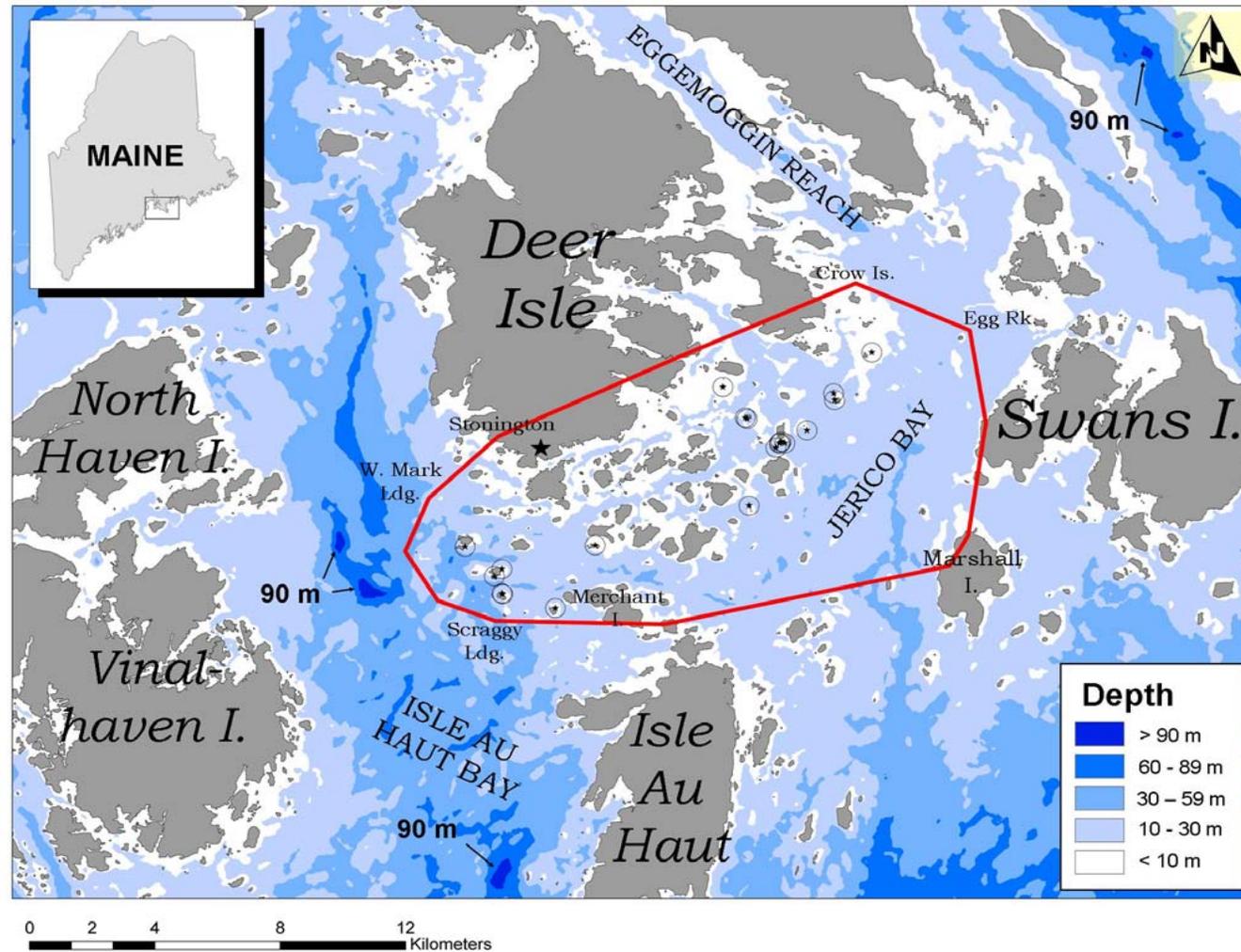
Figure 2.1. Location of research on diving behavior and activity for harbor seal pups near Stonington, Maine during 2004 and 2005. The s indicates the region where pups were captured and monitored using VHF radio telemetry. Deeper water (60 – 90 m) was located to the west and northeast of this area. The initial capture locations for study animals are shown as stars within a circle (⊙).
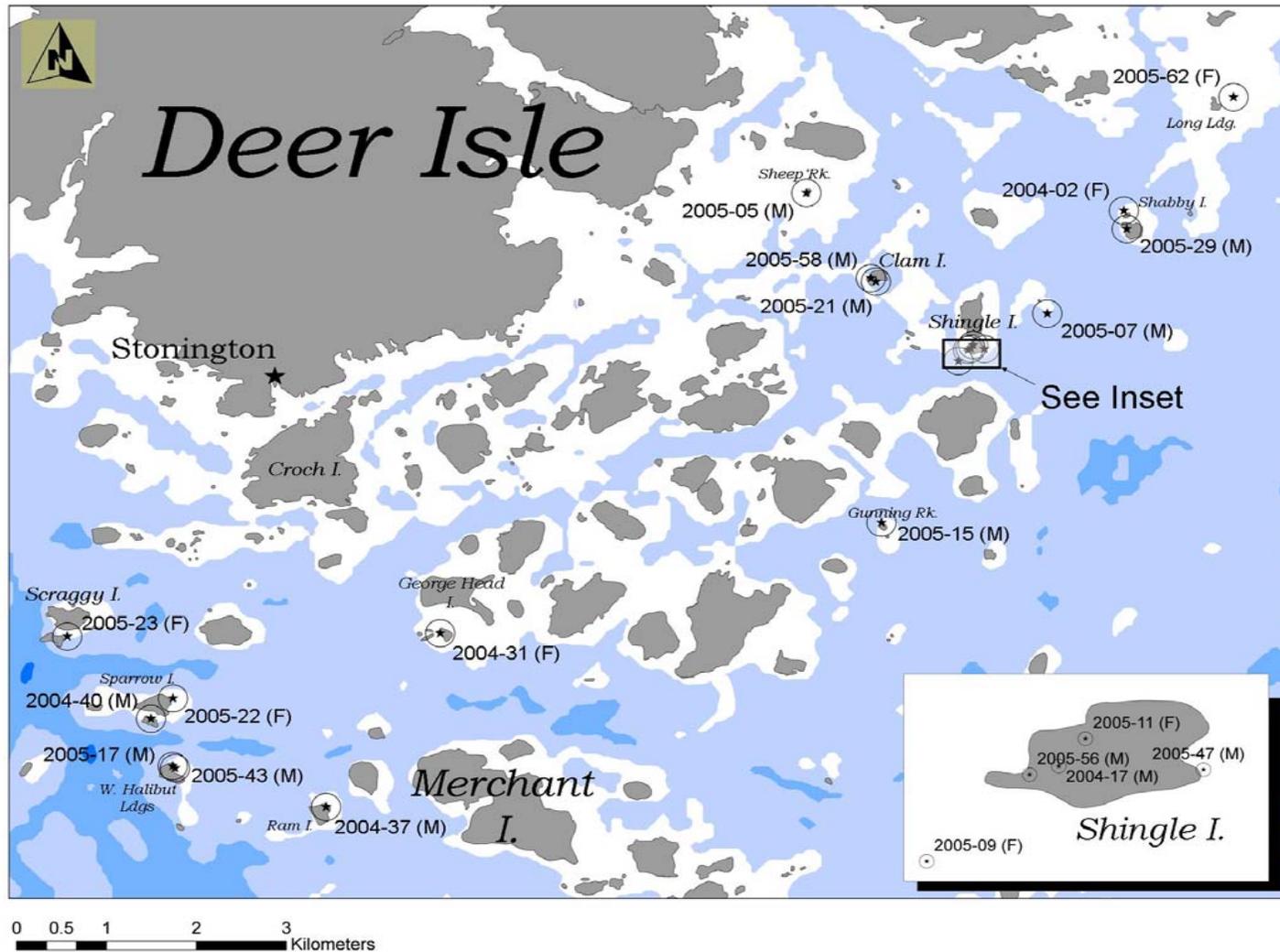
Figure 2.2. Initial capture locations (⊙) for harbor seal pups (*n* = 20) that were monitored using VHF radio telemetry and time-depth recorders during 2004 and 2005.

using a cyanoacrylate adhesive and bonder accelerant (Superbonder® 422 Adhesive and

Tak Pak® 7452 Accelerator, Loctite Canada Inc.,Mississauga, ON, Canada). The TDR

assembly was positioned on the lower back of each pup approximately 4 inches forward

of the tail to provide an "at depth" reading during most activity in water. Each TDR

assembly consisted of a TDR unit (LTD-1100 or 1110, Lotek Wireless Inc.) glued to the

cloth portion of an approximately 1.5" x 2" oval swath of ¼-inch cloth/neoprene material.

Two holes were placed in the neoprene on either side of the TDR and it was fastened

through the holes with a plastic cable tie (Appendix C). The neoprene rubber surface of

the assembly was glued to the fur. The advantage of this method of attachment was that

the TDR remained attached during deployment but was easily removed by separating the

cloth layer from the neoprene layer after cutting the cable tie. The two types of TDRs

used were programmed to record data differently. The LTD-1100 recorded data for

approximately 5 days at 14 second resolution while the LTD-1110 initially sampled at a

14s resolution but then began to overwrite data at a lower resolution once the memory

capacity was reached. After approximately 11, and 22 days, the LTD-1110 shifted

sampling to 28 and 56 s resolution respectively. As a result, the archived data varied in

resolution from 14s to 56s depending on the type of recorder and duration of deployment.

Both types of TDRs were designed to record temperature to the nearest 0.2 °C (± 0.3 °C)

and depth to the nearest 0.5 m (± 1.3 m).

Pups were relocated frequently during the deployment period using radio

telemetry (Cochran and Lord 1963). During each observation, the location of the pup was

estimated using the onboard WAAS-enabled GPS chart plotter or NOAA navigational

charts. At 5 to15 days after deployment each pup was recaptured, reweighed, and the

TDR was removed. The TDR was read after returning to port up to 6 hours later. Growth rate was estimated using the difference between final and initial mass divided by the number of days between captures. Birth mass was back-calculated by subtracting the rate of mass gain times the age from the initial capture mass. Weaning date was defined as the mean date between the last observation of pups with an adult and the next observation during which the pup was found alone. Pups observed to be alone on at least two additional occasions and having clear blood serum were reported to be weaned during the second capture. Capture mass for pups that were weaned could not be used to estimate mass gain rate or birth mass and therefore were not used in the analyses examining these factors.

TDR Data Interpretation – TDR data was downloaded using the software supplied by the manufacturer (Tagtalk 1100 v3.1, Lotek Wireless Inc.). For each TDR, the data was saved as a separate text file consisting of up to 68,000 lines with a time, temperature, and pressure observation per line. I imported these lines of text into a database and performed all data manipulations using Microsoft Access Visual Basic Code (VBA). Surface pressure readings drifted slightly between dives and considerably over the coarse of deployment making it necessary to provide a corrected zero reference value (surface value) before calculating depth. I considered the minimum value occurring within a window of six minutes before and after each observation to be the zero reference. I subtracted each pressure observation from the zero reference and divided the result by 1.46 to convert from pressure, in pounds per square inch, to depth, in meters.

The TDRs used in this research did not directly detect when a pup was hauled out. Based on pressure changes alone, it was not possible to delineate between periods spent hauled out on land and time spent inactive on the surface of the water. The status of a pup 'in water' or 'hauled out', therefore, was inferred from pressure and temperature readings. Readings at depths greater than 3 m (twice the resolution of the TDR) were classified as 'in dive' and were automatically assigned a status of 'in water'. Readings less than 3 m deep were considered 'surfaced' and to classify these remaining non-diving behaviors as 'in water' or 'hauled out', I used the classification decision tree shown in Figure 2.3. Temperature decreases less than or equal to -0.05 °C/s were associated with at depth readings (> 5 m); I used this value to signify a change to 'in water' status even if there was no corresponding pressure reading increase. During periods of stable temperature ($|\Delta T| < 0.01$ °C/s) outside the normal range of seawater temperatures, I classified the pup as 'hauled out'. Because seawater temperatures increase during the pupping season and vary by location, I used readings in the TDR record set at depths greater than 5 m and with stable temperature ($|\Delta T| < 0.01$ °C/s) to provide an estimate of the range of normal seawater temperatures. Finally, in the absence of other evidence the observation was classified the same as the previous case. The behavior defined in each case was assumed to occur for the entire time interval between observations. The proportion of time in water (PIW) and in dive (PID) were calculated as the total time classified as 'in water' divided by the total TDR observation period, and the time during which records were classified as 'in dive' divided by the total time classified as 'in water', respectively. These proportions were normalized using an arcsine square-root transformation prior to performing statistical analyses.
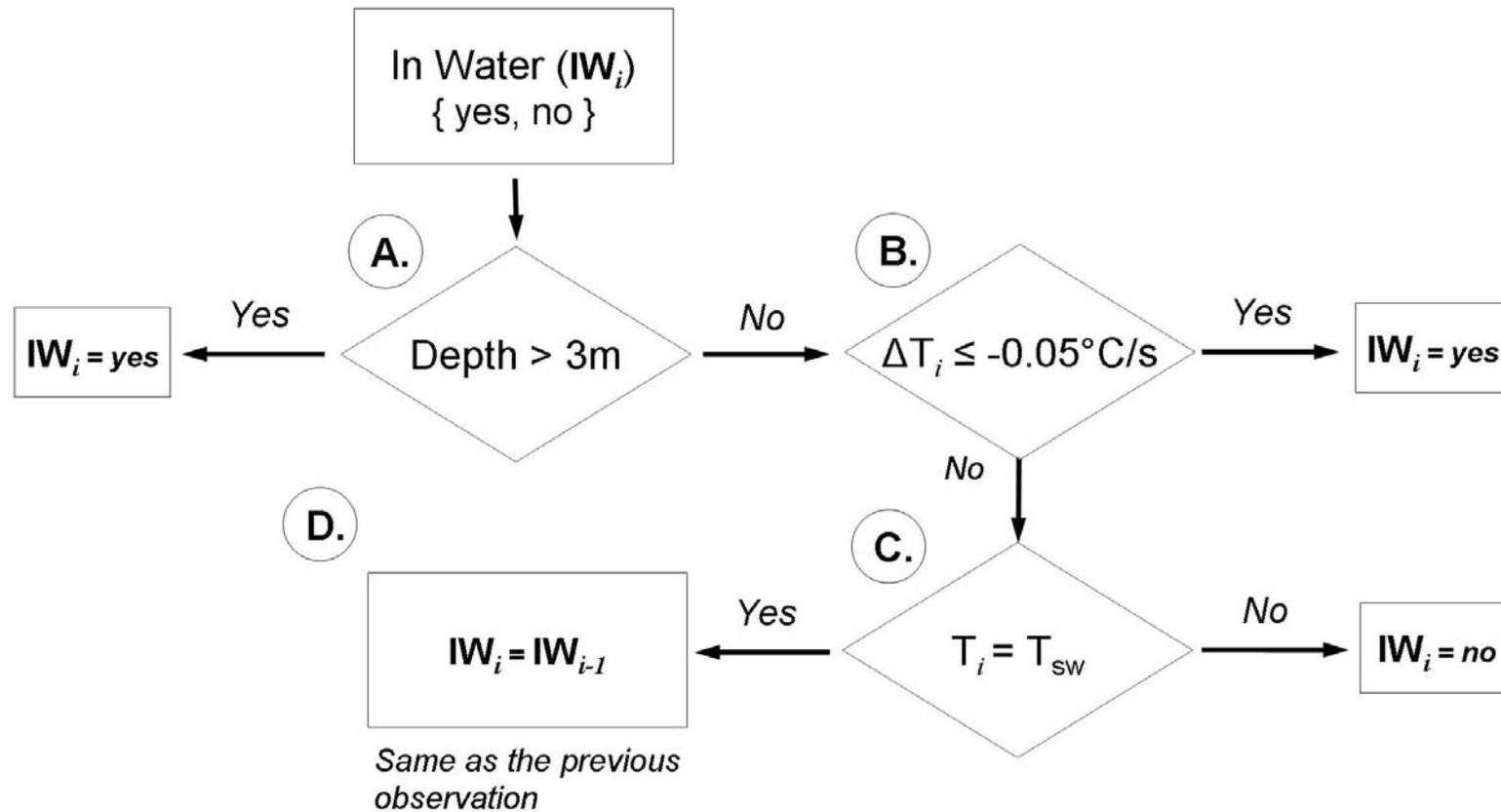
Figure 2.3. The classification decision tree used to classify each TDR record as 'in water' (IW_i = yes) or 'hauled out' (IW_i = no). Observations at depth >3 m were classified as in water (A.). Quick drops in temperature (B.) were considered evidence that the pup had entered the water. Cases with stable temperatures greater than or less than the range of normal seawater temperatures were considered to be out of water (C.). If there was otherwise insufficient evidence, the case was classified the same as the previous observation (D.).

Previous studies have included dives greater than 4 meters for analyses (Boness *et al.* 1999, Jorgensen *et al.* 2001). In this study, I translated depth readings into dive records by considering consecutive observations greater than 5 m deep to be a single dive. I chose this criteria since a surfacing event between two shallow dives was likely to be missed at the data resolution available. I considered a diving bout to have ended if more than 30 minutes passed without a dive occurring. The behavior information I extracted from the points within each dive are illustrated in Figure 2.4.

I defined dive depth as the maximum depth reading during the dive, dive duration as the number of observations below 5 m times the resolution of the data (seconds), and bottom time as the number of observations greater than 80% of the dive depth times the resolution. The proportion of bottom time was calculated as bottom time divided by dive duration. Dive duration and bottom time were not calculated for 245 dives recorded for Pup# 2005-43 since the data resolution was greater than 30s for these cases. Transit rate was calculated using the absolute value of the average change in depth per unit time when less than 80% of maximum dive depth. The post-dive surface interval (PDSI) was considered to be the period of time between end and beginning of consecutive dives within a diving bout. Tide state during the period of TDR observations was estimated using tide prediction algorithm software (WXTides32[1]) which provided a tide height value for every 10 minutes throughout the study period. These predictions were verified against local tide charts. Each dive record was associated with the closest tide record available.

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[1] Subordinate data for Stonington, Maine. WXtide32 version 4.5, rev 2006/03/09. Available at http://WXTide32.com
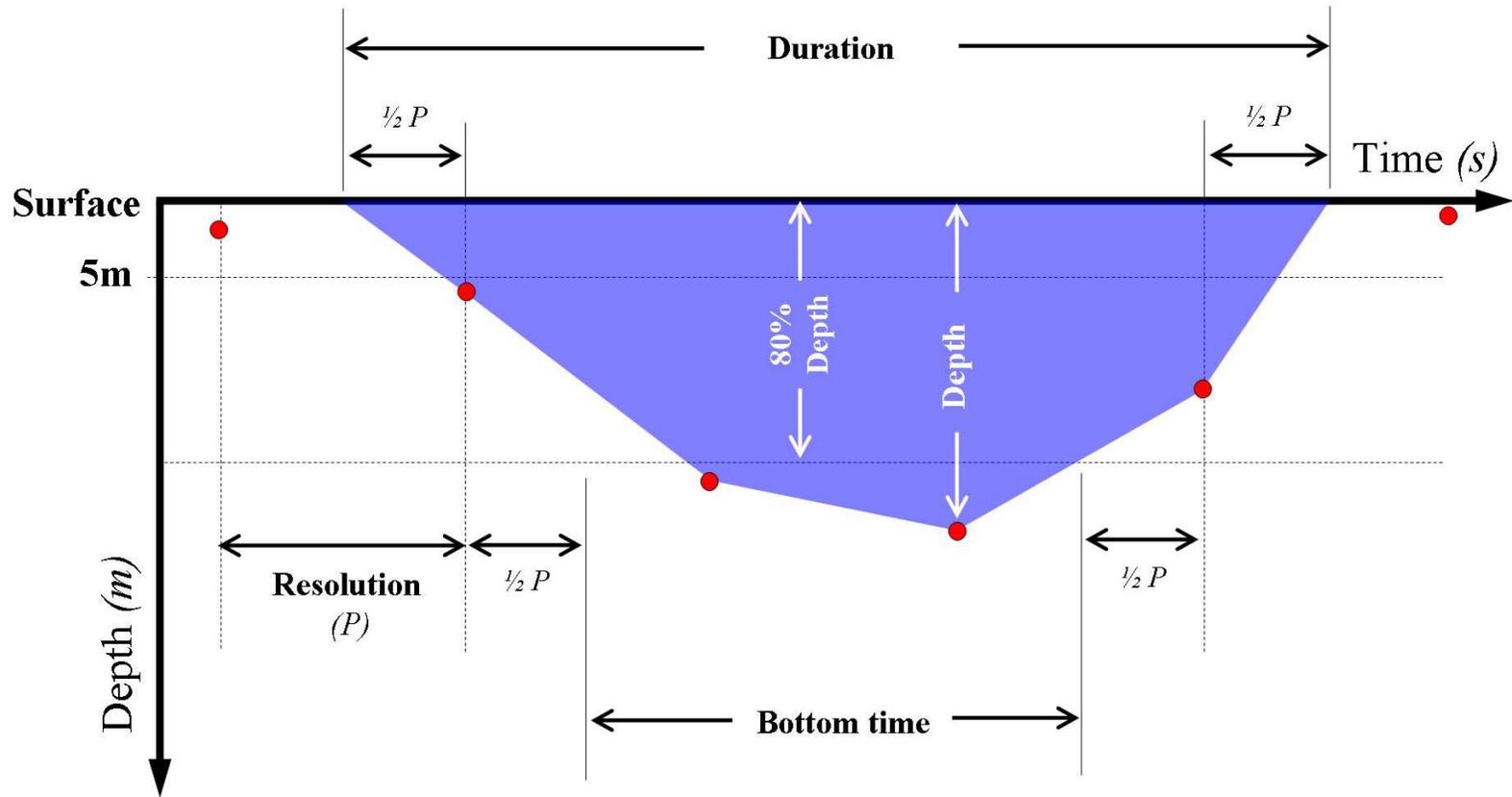
Figure 2.4. Summary of behavior information generated from TDR data. Dots (●) annotate TDR data points plotted on a time-depth profile. Records at depths greater than 5 m were considered a single dive and were used to calculate dive duration (four dots). Dive resolution (P) was the measure of the time interval between sample points. Dive depth was the maximum depth attained during a dive and all points ≥80% of this value were considered to be at the bottom of the dive. Dive duration and bottom time were calculated as the number of points in the dive and at the bottom, respectively times the data resolution.

Based on radio tracking data, nursing pups generally moved distances less than 2 km from the location previously observed (unpublished data, this study). I defined the home range of each pup to be the 2 km buffer around the minimum convex polygon of all relocations. I used ArcMap™ version 9 (ESRI® Inc., Redlands, CA, USA) to estimate the home range size and bathymetry available within each home range. A bathymetry grid of the study area was created by interpolating depths between contour lines within the shape file 'BATHYM100' at a 30x30 m resolution. 'BATHYM100' was downloaded from the Maine government website[1] and contained bathymetry lines at 10 m intervals for the entire Gulf of Maine at a scale of 1:100,000. I extracted the mean and maximum depths within each pup home range to be used as indices of depths available. Using the same criteria above, I also estimated the available depths within the minimum convex polygons around the observed movement of pups during four age periods; 0-5 dpp, 6-10 dpp, 11-15 dpp, and greater than 15 dpp.

Data Analyses – Dives occurring in the first six hours after deployment, one hour prior to recapture, or occurring in bouts of less than 10 dives were excluded from dive analyses. Analyses were carried out using a statistics software package (Systat® version 11, SYSTAT Software Inc., Richmond, California, USA). To examine changes in activity and dive behavior with age, I used analysis of variance (ANOVA) to test for significant differences in behavior across four age groups; 0-5, 6-10, 11-15, >15 dpp. Pups were randomly assigned to one group and only data falling within that age period was used. These age breaks were chosen so that roughly equal numbers would be included in each group. Pup behavior characteristics that were compared against these age groups

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[1] Maine Office of Geographic Information, Augusta, ME. Available at http://megis.maine.gov/catalog/

included: proportion of time in water, proportion of time spent diving while in water, mean dive frequency, mean PDSI, mean dive duration, maximum dive duration, mean dive depth, maximum dive depth, proportion of bottom time, mean transit rate, and maximum transit rate. Statistical significance of each ANOVA was determined after a Bonferroni (1935) correction was applied to account for multiple comparisons. Comparisons between age groups were made *a posteriori* using Tukey's HSD tests (Zar 1999). I tested for homogeneity between age groups (Bartlett's test, Snedecor and Cochran, 1967) and, when necessary, variance was equalized by transforming the response using the natural logarithm.

For the subset of nursing pups that had a valid mass gain rate and birth mass estimate, I used generalized linear models to explain differences in activity and diving behavior. A separate model was developed for each response variable (proportion of time in water, proportion of time diving, mean dive frequency, mean dive duration, mean dive depth, proportion of bottom time, mean transit rate, maximum dive duration, maximum dive depth, and maximum transit rate) to test the effects of birth mass, mass gain rate, sex, age, tide height, mean and maximum depth available. Data for the entire TDR deployment period was considered a unit of observation in the model. Significant models were chosen using backwards stepwise selection using an alpha of 0.05 as the criteria to retain a parameter in the model. Because of a limited sample size, interactions between factors were not tested. For each independent variable, I checked for normality using frequency distribution plots and significance tests (Shapiro and Wilk, 1965). The residuals of each model were examined for normality (Looney & Gulledge, 1985) and when this assumption was not met, a transformation of the response using the natural

logarithm was used to correct the problem. Finally, I examined the relationship between the maximum depths achieved by each pup and the maximum depth available within the four age groups previously described. Simple linear regression was used to test for a significant correlation between depth achieved and depth available for each of these groups.

RESULTS

Of thirty-eight deployments, useable dive data was attained from twenty TDRs during two seasons (Table 2.1). A total of 40,548 dives were analyzed for 20 pups. Pup home ranges averaged 36.3 km^2 but varied by an order of magnitude across individuals (Table 2.2, range 13.6- 123.5 km^2). Mean depth available within these home ranges was relatively constant (mean = 17.3m, range: 9.5 - 38.4m), however, maximum depths available were widely varied (mean = 44, range: 23 - 97m). Because home ranges were centered on haul out sites, maximum depth tended to increase with home range size (linear regression, $y = 2.66 + 0.31 \cdot x$, $r^2 = 0.15$, p = 0.05). Initial capture age varied from 0 to 9 dpp with a mean of 4.5 dpp. Due in part to the difficulty of recapturing some animals, recapture age ranged from 9 to 32 dpp with a mean of 17.2 dpp (Table 2.2). The mean age of pups that were captured before they were weaned was 14.8 dpp. A summary of behavior characteristics for pups over the entire duration of TDR deployment is shown in Table 2.3.

Table 2.1. The outcome for the deployment of time depth recorders on pups during 2004 and 2005 in Maine.

Deployment Outcome	2004	2005	Total	Percent of TDRs Deployed
TDR malfunction	1	3	4	11%
Attachment failed	0	1	1	3%
Pup missing	2	1	3	8%
Pup abandoned	2	3	5	13%
Failed to recapture	0	5	5	13%
Useable data	5	15	20	52%
Total Deployments	10	28	38	

Changes in behavior with Age – Pups were active in the water 61% of the time and while in water the were diving 39% of the time (Table 2.3). The average proportion of time spent in water tended to decrease from 0-5 dpp to 5-10 dpp and then increased in subsequent age groups, however, this trend was not significant (ANOVA, $F_{3,16}$ = 2.41, p = 0.11). There was no change in the proportion of time diving ($F_{3,16}$ = 1.88, p = 0.17) or diving rate ($F_{3,16}$ = 0.59, p = 0.63) as pups got older. PDSI tended to decrease between ages 0 and 15 dpp and then increased sharply after age 15 dpp ($F_{3,16}$ = 3.50, p = 0.04) although this trend was not significant after adjusting the significance level for multiple comparisons (Table 2.4). Mean and maximum dive duration increased with age (Figure 2.5, $F_{3,16}$ = 8.09, p<0.01 and $F_{3,16}$ = 6.45, p<0.01 respectively). Mean dive duration significantly increased from 53s at 6-10 dpp to 74s by the end of lactation (Tukey's HSD, p<0.001). Maximum dive duration was similar from ages 0 and 15 dpp, and increased by

Table 2.2. Summary of capture and deployment period characteristics for pups captured and equipped with time-depth recorders in Maine during 2004 and 2005.

Year and No.	Sex	Initial Capture Date	Age Interval *(dpp)*	Age Weaned *(dpp)*	Duration *(days)*	Birth Mass *(kg)*	Gain Rate *(kg/d)*	Depths Available *(m)*		Home Range Size *(km²)*
								Mean	Max.	
2004-02	F	May 12	3 - 17	20	14	8.0	0.39	15	31	31.8
2004-17	M	May 21	3 - 13	19	10	10.9	0.50	13	31	24.7
2004-31 [a]	F	May 31	0 - 12	13	12	11.6	0.20	20	62	39.9
2004-37 [a]	M	Jun 01	5 - 16	>26	11	10.6	0.64	26	62	26.4
2004-40 [b]	M	Jun 04	5 - 13	>26	8	10.7	0.58	17	62	123.5
2005-05 [a]	M	May 09	3 - 12	>15	9	12.3	0.38	10	23	17.8
2005-07	M	May 14	2 - 19	32	17	11.3	0.54	16	62	59.2
2005-09	F	May 14	1 - 14	27	13	11.3	0.51	14	31	22.2
2005-11	F	May 16	4 - 15	18	11	8.8	0.29	14	31	14.2
2005-15	M	May 17	4 - 19	26	15	10.6	0.36	17	43	83.1

[a] TDR data only available for first 5 days of deployment.
[b] No umbilicus at time of capture, age estimated using a predictive model.
[c] Pup weaned before second capture.

Table 2.2. Continued.

Year and No.	Sex	Initial Capture Date	Age Interval (dpp)	Age Weaned (dpp)	Duration (days)	Birth Mass (kg)	Gain Rate (kg/d)	Depths Available (m) Mean	Max.	Home Range Size (km²)
2005-17	M	May 17	1 - 11	26	10	12.6	0.58	16	62	66.9
2005-21	M	May 18	3 - 15	>20	12	11.9	0.17	13	28	39.8
2005-22	F	May 18	1 - 14	>26	13	11.4	0.61	22	62	23.5
2005-23	F	May 20	1 - 13	32	12	9.8	0.63	38	97	25.6
2005-29 [a]	M	May 27	3 - 9	30	6	12.0	0.39	15	26	13.6
2005-43 [c]	M	May 31	3 - 25	23	22	N/a	0.14	25	62	18.1
2005-47 [b,c]	M	Jun 02	16 - 32	23	16	N/a	0.04	13	31	34.5
2005-56 [a]	M	Jun 05	9 - 24	27	15	11.0	0.09	16	31	17.6
2005-58 [b,c]	M	Jun 05	9 - 22 [b]	19	13	N/a	0.22	11	26	22.4
2005-62 [c]	F	Jun 11	14 - 29 [b]	25	15	N/a	0.05	14	31	21.8

[a] TDR data only available for first 5 days of deployment.

[b] No umbilicus at time of capture, age estimated using a predictive model.

[c] Pup weaned before second capture, mass gain rates not usable.

Table 2.3. Summary of the behavior and activity recorded by time-depth recorders deployed on individual harbor seal pups during 2004 and 2005 in Maine.

Year & Seal No.	Mean Age (dpp)	Dives	pIW[a]	pID[b]	Dive Frequency (hr⁻¹)	PDSI[c] (sec)	Duration (min)	Depth (m)	pBT[d]	Transit Rate[e] (m/s)
2004-02	13.6	1762	0.55	0.19	31.6	82.5	0.62 (2.34)	8.3 (26.6)	0.90	0.33 (0.97)
2004-17	9.6	1564	0.62	0.37	30.5	70.1	0.85 (2.81)	10.8 (25.5)	0.78	0.46 (1.45)
2004-31	5.0	594	0.54	0.37	26.4	93.7	0.59 (2.11)	8.5 (30.3)	0.81	0.37 (1.01)
2004-37	5.1	1388	0.73	0.39	21.2	94.2	1.08 (2.81)	12.3 (55.5)	0.79	0.41 (1.52)
2004-40	7.5	2847	0.74	0.52	24.5	68.7	1.23 (3.99)	13.9 (64.5)	0.70	0.44 (1.49)
2005-05	5.0	1026	0.50	0.33	28.1	77.7	0.80 (2.34)	9.2 (21.8)	0.81	0.38 (1.19)
2005-07	16.7	2542	0.68	0.26	25.8	82.4	1.08 (3.28)	10.1 (44.2)	0.85	0.29 (1.23)
2005-09	12.5	2211	0.64	0.49	26.7	90.1	0.87 (2.81)	8.2 (29.7)	0.88	0.31 (1.25)
2005-11	10.5	876	0.44	0.27	32.6	69.0	0.78 (2.81)	9.7 (30.5)	0.81	0.40 (1.34)
2005-15	14.7	3847	0.68	0.53	29.6	65.9	0.98 (4.22)	10.7 (41.6)	0.84	0.35 (1.71)

[a] Proportion of time spent in water
[b] Proportion of time in water spent diving
[c] Mean post-dive surface interval
[d] Proportion of bottom time
[e] Absolute value in the change in depth per second when >5 m and <80% of maximum dive depth

Table 2.3. Continued.

Year & Seal No.	Mean Age (dpp)	Dives	pIW[a]	pID[b]	Dive Frequency (hr^{-1})	PDSI[c] (sec)	Duration (min)	Depth (m)	pBT[d]	Transit Rate[e] (m/s)
2005-17	5.9	1575	0.62	0.26	25.3	92.1	0.94 (4.22)	10.2 (30.3)	0.78	0.36 (1.28)
2005-21	8.5	2044	0.52	0.45	25.4	86.4	0.89 (3.99)	10.4 (31.4)	0.81	0.39 (1.28)
2005-22	7.3	2052	0.54	0.52	21.8	94.9	0.95 (3.99)	9.2 (42.8)	0.87	0.31 (1.36)
2005-23	7.0	3401	0.70	0.31	24.2	103.5	0.70 (2.81)	10.7 (53.1)	0.83	0.39 (1.51)
2005-29	5.9	201	0.39	0.45	24.7	90.7	0.71 (2.11)	6.1 (15.1)	0.95	0.20 (0.82)
2005-43	16.2	2793	0.64	0.48	23.0	85.8	1.18 (4.69)	11.4 (58.3)	0.82	0.26 (1.44)
2005-47	24.4	2299	0.71	0.52	23.3	69.7	1.47 (4.69)	11.9 (37.2)	0.82	0.35 (1.41)
2005-56	11.7	558	0.45	0.21	31.4	61.2	0.94 (2.58)	10.2 (29.1)	0.79	0.40 (1.10)
2005-58	15.9	2778	0.67	0.51	24.5	86.4	1.07 (4.69)	14.1 (99.5)	0.77	0.40 (1.72)
2005-62	21.3	4190	0.76	0.60	26.6	72.7	1.14 (4.22)	13.9 (100.4)	0.76	0.38 (1.69)

[a] Proportion of time spent in water
[b] Proportion of time in water spent diving
[c] Mean post-dive surface interval
[d] Proportion of bottom time
[e] Absolute value in the change in depth per second when >5 m and <80% of maximum dive depth

Table 2.4. Results of multiple one-way ANOVA comparisons of pup activity and dive behavior observed among four age groups ($n = 20$) during 2004 and 2005 in Maine.

Response Variable	Transformation	Trend	r^2	$F_{3,16}$	Prob.	Adj. Prob.[a]
Mean Behavior						
proportion of time in water (PIW)	arcsine square-root	increasing	0.31	2.41	0.11	1.00
proportion of time in dive (PID)	arcsine square-root		0.26	1.88	0.17	1.00
dive frequency (DR)	logarithm		0.10	0.59	0.63	1.00
post-dive surface interval (PDSI)	logarithm	decreasing	0.40	3.50	0.04	0.48
dive duration (DT)	logarithm	increasing	0.60	8.09	<0.01	0.02
dive depth (DP)	logarithm	increasing	0.23	1.56	0.24	1.00
transit rate (TR)		increasing	0.06	0.34	0.80	1.00
proportion of bottom time (PBT)	arcsine square-root		0.03	0.17	0.92	1.00
bottom time (BT)	logarithm	increasing	0.62	8.74	<0.01	0.01
Maximum Behavior						
dive duration (DT_{mx})	logarithm	increasing	0.55	6.45	<0.01	0.05
dive depth (DP_{mx})		increasing	0.32	2.51	0.10	1.00
transit rate (TR_{mx})	logarithm		0.08	0.46	0.72	1.00

[a] Bonferroni (1935) adjusted probability.
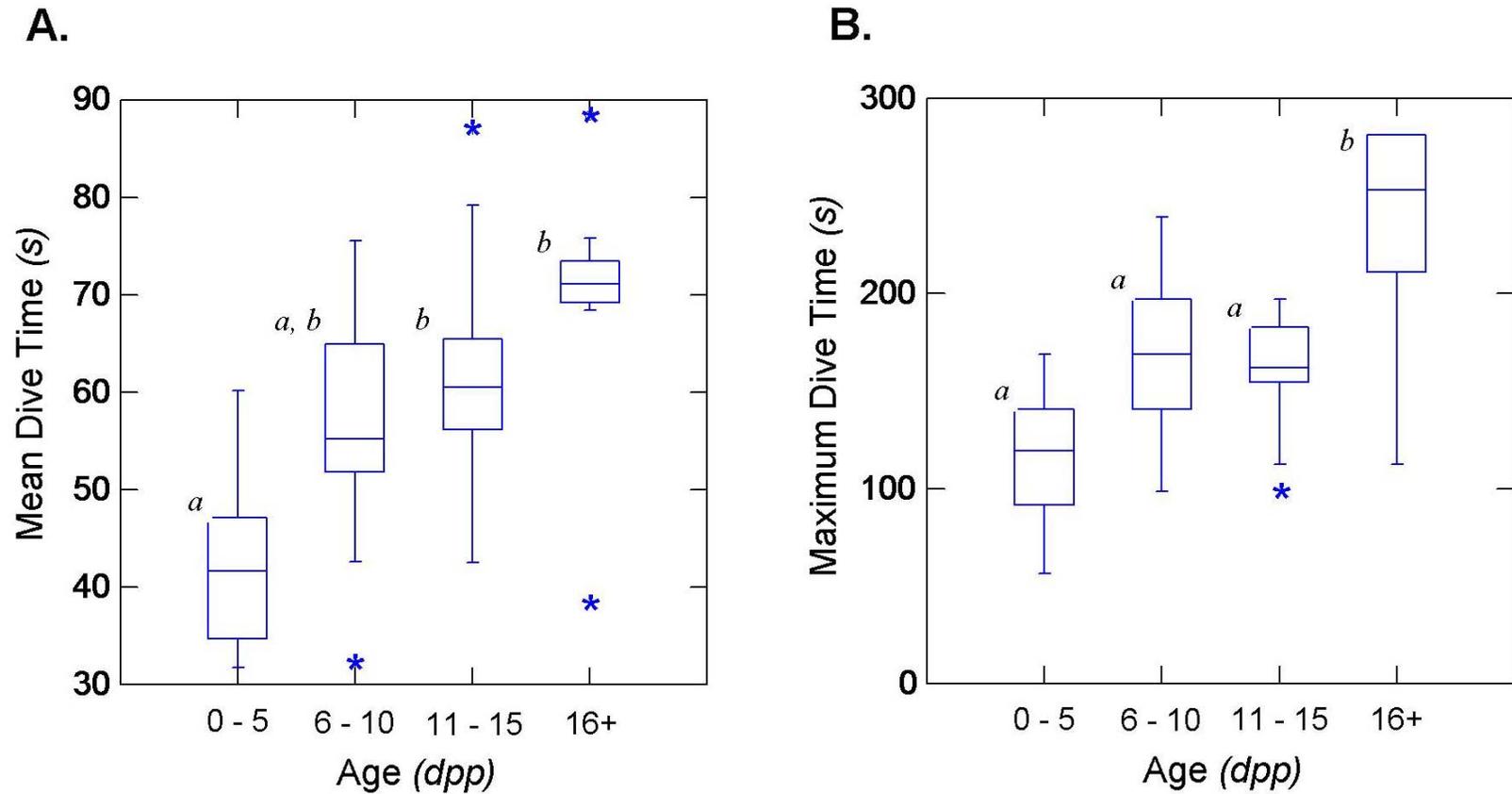
Figure 2.5. Mean (**A**; ANOVA, $n = 20$, $F_{stat} = 8.09$, $p = 0.02$) and maximum (**B**; $F_{stat} = 6.45$, $p = 0.05$) dive duration observed among four age groups of harbor seal pups in Maine during 2004 and 2005. Horizontal lines are medians, boxes delineate quartiles, vertical lines illustrate range of data excluding outliers (*). Groups annotated with similar letters were not found to not be significantly different using Tukey's pair-wise comparisons.

only 25s during that interval. By late lactation and into weaning, average maximum dive duration for all pups was 248s, which was a significant change from a 163s average at 15 dpp (Tukey's HSD, $p = 0.02$) and higher than the maximum values observed in any prior age group (239s). The longest dive observed in this study lasted 281s (Pup No. 2005-43, Age = 17 dpp) and was associated with a depth of 89m.

Early in lactation, pups were achieving 8.9 m in an average dive but were capable of dives as deep as 29 m based on maximum achieved dive depths. By weaning, average diving depth was 12 m and maximum dives averaged 60 m across individuals. Maximum depths observed during each age interval were: 32 m between 0-5 dpp, 65 m between 6-10 dpp, 60 m during 11-15 dpp, and 100 m after 15 dpp. Although, mean and maximum depth tended to increase with age, this trend was not significant across age intervals ($F_{3,16}$ = 1.56, $p = 0.24$ and $F_{3,16} = 2.51$, $p = 0.10$, respectively). Similar to dive duration, mean bottom time increased significantly with age ($F_{3,16} = 8.74$, $p<0.01$) with a significant difference observed between ages 6-10 dpp and >15 dpp (Figure 2.6A, Tukey's HSD, $p = 0.02$). Proportion of bottom time, mean and maximum transit rate were not significantly different among age groups. Although maximum transit rate did not differ significantly among the four age groups, inspection of this relationship suggested that there was an increase in transit rate after age 5 dpp (Figure 2.6B). I re-examined age related changes in mean and maximum transit rate by performing a pair-wise comparison of data for 15 pups that had diving data during both 0-5 dpp and 6-10 dpp. These analyses revealed that there was a significant increase in mean (paired t-test, df = 14, t_{stat} = 5.19, $p<0.01$) and maximum ($t_{stat} = 6.03$, $p<0.01$) transit rates early in lactation.

A.

B.
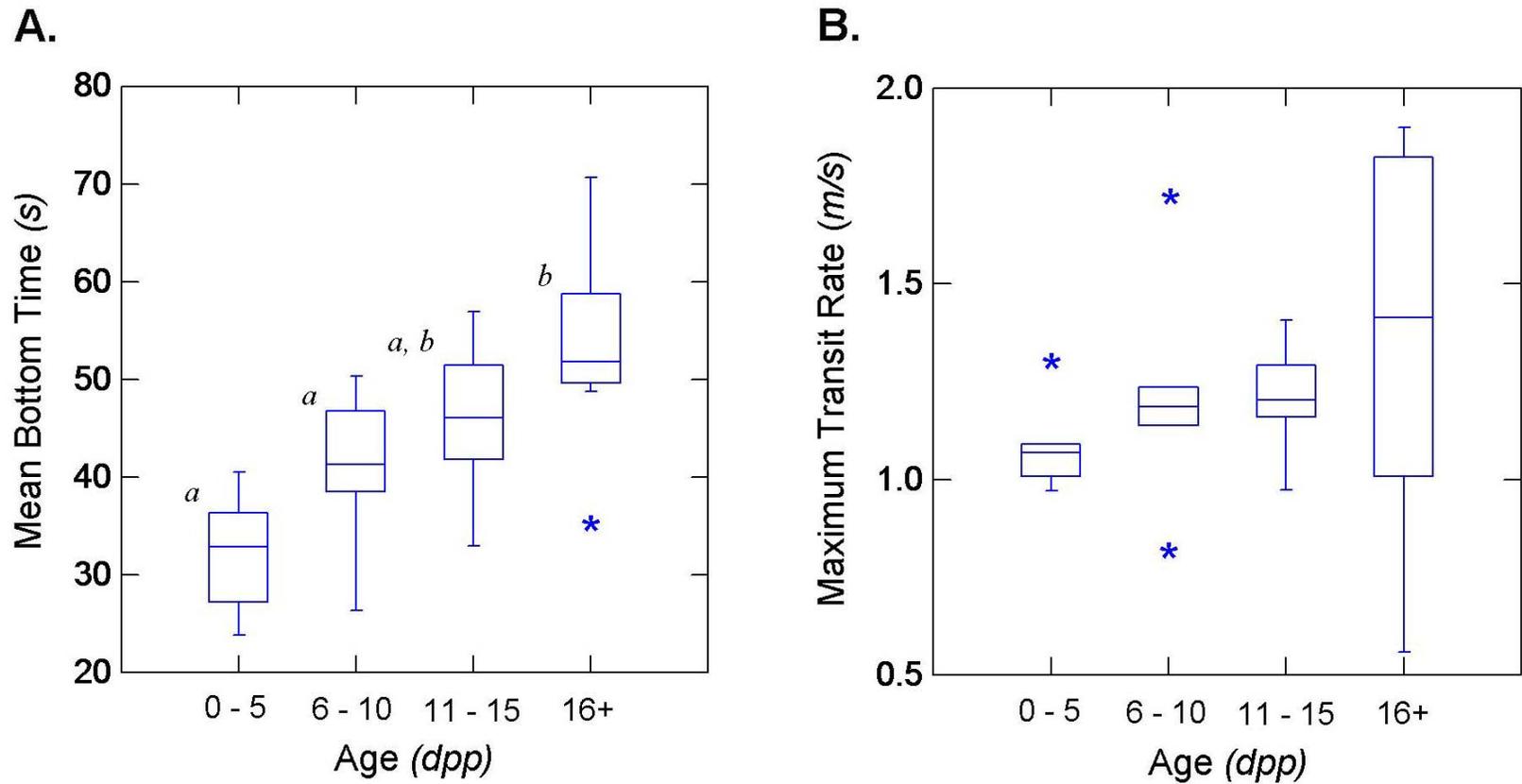
Figure 2.6. Mean bottom time (**A**; ANOVA, $n = 20$, $F_{stat} = 8.74$, $p = 0.01$) and maximum transit rate (**B**; $n = 20$, $F_{stat} = 0.46$, $p = 0.7$) observed among four age groups of harbor seal pups in Maine during 2004 and 2005. Horizontal lines are medians, boxes delineate quartiles, vertical lines illustrate range of data excluding outliers (*). Groups annotated with similar letters were not found to not be significantly different using Tukey's pair-wise comparisons.

Factors Influencing Activity and Dive Behavior – Four pups were likely weaned prior to

TDR recovery and mass gain rates could not be used to back calculate their birth mass

(Table 2.2). Additionally, for two individuals the TDR data only spanned 50% of the

deployment period and I considered their mass gain rates to be unrepresentative of their

development during the period of TDR data collection. For the remaining 14 pups

(9M:4F), mass gain rate was 0.47 kg/d (S.E.= 0.04, range: 0.17 – 0.64 kg/d) and mean

birth mass was 10.9 kg (S.E. = 0.35, range: 8.0 – 12.6 kg). There was no difference in

growth rate between sexes (two sample t-test, t_{stat} = 0.34, p = 0.73), however, estimated

birth mass was higher for males (t_{stat} = -2.61, p = 0.02). Several independent variables

used in the models were highly correlated. The two worst cases of colinearity occurred

between birth mass with sex (r = 0.60) and growth rate with maximum depth available (r

= 0.77). To reduce the problems in model selection associated with multi-colinearity,

models were run in two batches including only one of the two collinear variables at a

time. Of the backwards selected models in each batch, the adjusted-r^2 fit was used to

select the best model and any variables excluded in that batch were then tested.

The best fit model for each behavior is summarized in Table 2.5. The proportion

of time that pups spent in the water was highly influenced by mass gain rate after

controlling for tide height and pup age (r^2_{adj} = 0.81, p<0.001). Mass gain rate taken alone

was a significant factor and explained 40% of the variation in the proportion of time pups

spent in water (Figure 2.7). This pattern was consistent for all pups with the exception of

Pup No. 2005-21 (studentized residual = -4.510). Despite being consistently observed

with an adult, this pup had an abnormally low growth rate during the TDR deployment

Table 2.5. Generalized linear models produced using backwards stepwise selection showing the significant factors describing the activity and dive behavior of nursing harbor seal pups monitored by TDR ($n = 14$) during 2004 and 2005 in Maine. Factors that were tested included pup birth mass (bM), mass gain rate (mGR), mean age (A), mean tide height (Th), mean depth available (mDA), and maximum depth available (DA_{max}).

Response Variable	Transformation	Model	r^2adj.[a]	Prob.
Mean Behavior				
proportion of time in water (PIW)	arcsine square-root	$y = -0.19 + 0.09 \times Th + 0.39 \times mGR + 0.04 \times A$	0.81	<0.01
proportion of time in dive (PID)	arcsine square-root	no significant effects (n.s.)		
dive frequency (DR)	logarithm	$y = 4.85 - 0.07 \times bM - 0.29 \times mDA$	0.70	<0.01
post-dive surface interval (PDSI)	logarithm	$y = 4.12 - 0.04 \times A + 0.23 \times mDA$	0.50	0.01
dive duration (DT)	logarithm	$y = 1.41 + 0.14 \times bM + 0.71 \times mGR + 0.09 \times A$	0.54	0.01
dive depth (DP)		$y = -5.69 + 1.77 \times Th + 0.56 \times A$	0.41	0.02
transit rate (TR)		n.s.		
proportion of bottom time (PBT)	arcsine square-root	n.s.		
bottom time (BT)	logarithm	$y = 1.55 + 0.11 \times bM + 0.57 \times mGR + 0.08 \times A$	0.63	<0.01
Maximum Behavior				
dive duration (DT_{mx})	logarithm	$y = 1.81 + 0.15 \times bM + 0.10 \times A + 0.27 \times DA_{max}$	0.52	0.02
dive depth (DP_{mx})		$y = -60.12 + 25.83 \times DA_{max}$	0.64	<0.01
transit rate (TR_{mx})		n.s.		

[a] The r^2 value presented is adjusted for the number of model parameters.
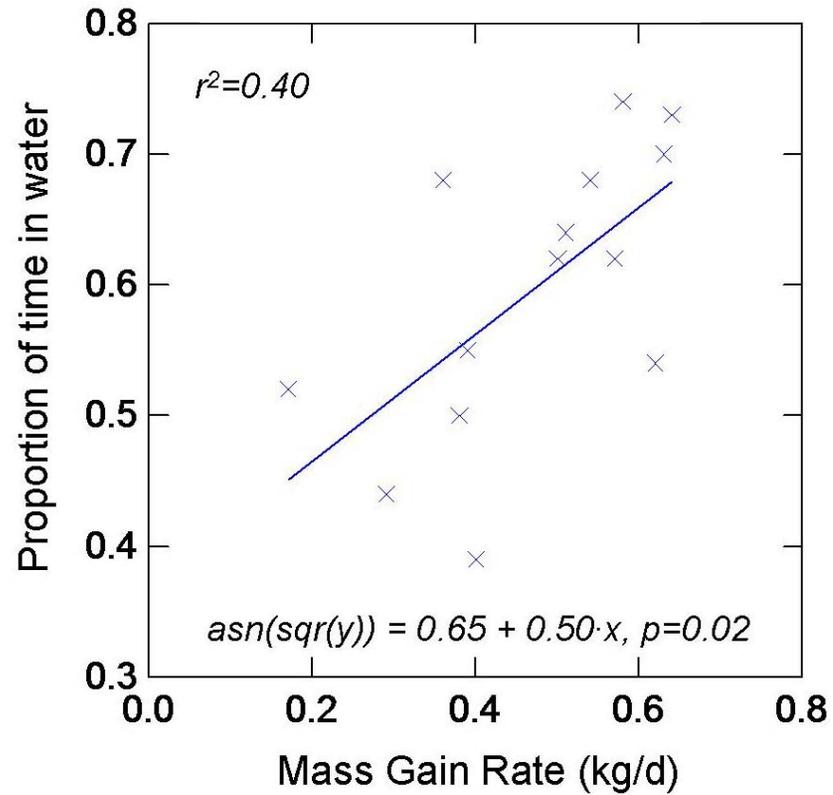
Figure 2.7. Correlation between nursing harbor seal pup mass gain rates and the proportion of time they spent in the water measured during TDR deployments conducted in Maine during 2004 and 2005.

period (mass gain rate = 0.17 kg/d). After removing this pup to examine its influence in the model, there was an increase in the coefficient for mass gain rate and an improved model fit ($y = -0.20 + 0.10{\times}Th + 0.48{\times}mGR + 0.04{\times}A$, $r^2_{adj} = 0.94$). The overall time that pups spent diving while they were in water was not significantly correlated with any of the factors modeled. Dive frequency tended to be lower for pups that resided in areas having a greater mean depth after controlling for a negative correlation between rate and pup size ($r^2_{adj} = 0.70$, $p < 0.01$). As pups aged, they spent less time at the surface following a dive but tended to rest longer when the mean depth available was greater ($r^2_{adj} = 0.52$, $p = 0.01$). The mean duration of dives was positively correlated with pup birth mass and mass gain rate after controlling for age ($r^2_{adj} = 0.54$, $p = 0.01$). Similarly, these same factors explained differences in bottom time ($r^2_{adj} = 0.63$, $p < 0.01$). Maximum dive duration was positively correlated with birth mass and maximum depth available after controlling for pup age ($r^2_{adj} = 0.52$, $p = 0.02$).

Mean dive depth was positively associated with tide height and tended to increase with age ($r^2_{adj.} = 0.41$, $p < 0.02$). Without controlling for tide height which explained 17% of the variation in dive depth, age was not a suitable predictor of dive depth ($t_{stat} = 0.87$, $p = 0.4$, $r^2 = 0.06$). When factors were tested individually, maximum depth available singly accounted for 23% of the variation in observed mean dive depth ($y = 1.5 + 2.3x$, $p = 0.05$). There was no correlation between mean dive depth and mean depth available ($r^2 = 0.02$, $p = 0.27$). The maximum depths achieved by pups were strongly correlated with maximum depth available within their home range ($r^2 = 0.64$, $p < 0.01$). Pup# 2004-40 dove deeper than predicted by depth available (studentized residual = 2.90). This pup, coincidentally, had the largest home range size (123.5 km^2) with an extent that covered

an area four-fold greater than the median observed home range size for all pups (25.6

km^2). Percent bottom time, mean and maximum transit rates were not significantly

influenced by the factors I tested.

The maximum depths to which pups dove during the first half of lactation were

correlated with the maximum depth available (Figure 2.8A). Between ages 0-5 dpp,

maximum dive depths averaged 49% (S.E. = 0.05) and were significantly associated with

the depths available within 2 km of all relocations ($y = -13.3+9.2x$, $r^2 = 0.32$, $p = 0.02$).

By ages 6-10 dpp, this relationship had strengthened considerably ($y = -62.8 + 25.6x$, $r^2 =$

0.55, $p < 0.01$) as pups on average were achieving 75% (S.E. = 0.05) of the depth

available in their designated home range. After ages 10 dpp, there was no significant

relationship between depths available and depths achieved (Figure 2.8B). This age related

change in the relationship between maximum dive and available depths was likely

associated with pup increasing their unobserved movements outside of the 2 km buffer I

used to define depth available (Table 2.6).
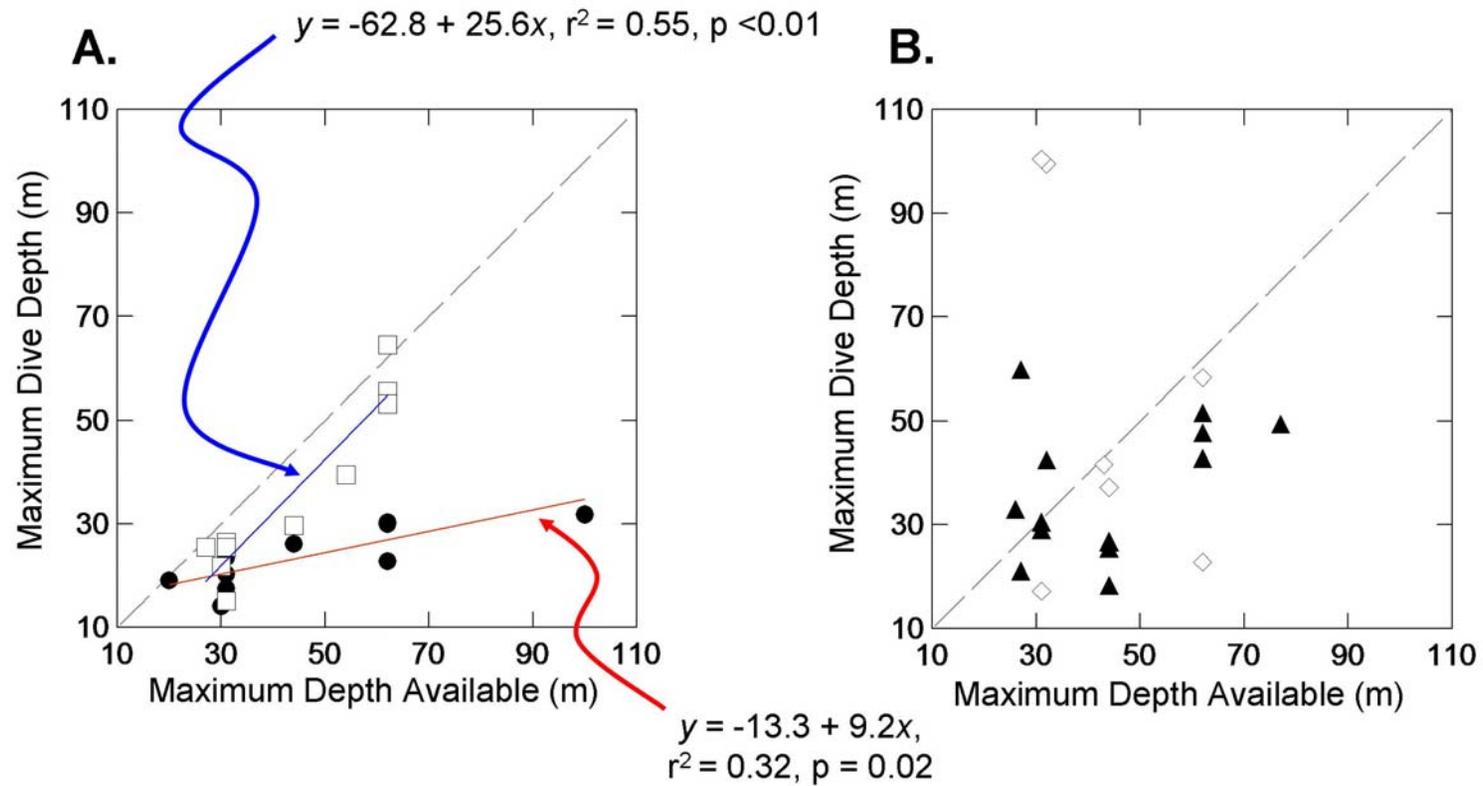
Figure 2.8. Maximum diving depth recorded for pups relative to the depth available in their designated home ranges during four age intervals: 0-5 dpp (solid-circle), 6-10 dpp (open-square), 11-15 dpp (solid-triangle), and >15 dpp (open-diamond). There was a significant correlation between maximum dive depth and maximum depth available in the two age groups that included pups less than 10 dpp (**A**), however, this correlation was not evident in data from older animals (**B**).

Table 2.6. The number (percent) of days that pups dove deeper than the depths available within the area designated as their home range (DA_{max}) during five age intervals.

Age (dpp)	> DA_{max}	≤ DA_{max}	No. TDR-Pup days
0 - 5	0	43 (100%)	43
6 - 10	0	77 (100%)	77
11 – 15	3 (5%)	64 (95%)	67
16 – 20	7 (25%)	21 (75%)	28
> 20	8 (27%)	22 (73%)	30
Total	18 (7%)	227 (93%)	245

DISCUSSION

Horning and Trillmich (1997) suggested that, "maximum dive depths and durations are rare performance extremes and as such reflect the absolute abilities of animals of different ages better than any other dive behavior parameter". Especially in nursing pups, measures of maximal behavior are not representative of true ability but rather provide indices of ability. Thus, in this study I use maximal behaviors to examine potential factors constraining dive ability. In contrast, mean behavior is the culmination of many decisions made over the long term. Factors having a subtle but chronic influence may not constrain a pup's behavior outright but would affect the mean expression of that behavior -- the statistical significance of which is easily determined with the large sample sizes provided using current TDR technology.

I examined the age related development of pup diving behavior during the lactation period using two approaches. The first method, using an ANOVA, was an attempt to explain changes in behavior purely on the basis of age. Sample size and the magnitude of changes in behavior with age influenced the results of this method due to the constraints of statistical power. Also, in cases where other factors (*i.e.,* unincorporated covariates) are important determinants of pup behavioral or physiological development, this method would likely fail to see a difference. A second approach compared mean and maximal behaviors over the entire TDR monitoring period with age and other factors. This could only be done with a subset of animals ($n = 14$) since the covariates examined were not available for all individuals. In these generalized linear models, age was found to describe pup behaviors in nearly the same way as the ANOVA analyses. An exception was a significant positive age effect on the proportion of time in water found in the GLM analysis that was not significant in the ANOVA.

Nursing seal pups previously have been reported to increase their time in the water with age. This is evident in bearded seals (Lydersen *et al.* 1994), ringed seals (Lydersen and Hammill 1993), and harbor seals (Jorgensen *et al.* 2001). The influence of natal habitat on pup behavior is apparent when comparing haul-out behavior across the species with active pups. Harbor seal pups spend more time in the water with increasing tide height. This was not observed in species using haul outs composed of ice (Lydersen *et al*. 1994, Lydersen and Hammill 1993). The evolutionary forces driving the extremely precocial behavior observed in harbor seal pups is likely strong because haul-out substrate is limited during high tide.

Similar to the findings of Jorgesen *et al*. (2001), mean bottom time and dive duration of harbor seal pups increased with age. This trend has been shown in precocial, nursing pups of other species (Lydersen *et al*. 1994, Lydersen and Hammill, 1993). The largest change in mean and maximum dive duration occurred between mid and late-lactation. Bottom time also increased with age, consistent with the previous findings (Jorgensen *et al*. 2001). Bottom time, however, was consistently about 83% of the total duration of a dive and did not change with age. This suggests that increases in dive transit time (*i.e.,* total travel time to and from the bottom of the dive) were proportional to the increased time that pups spent at the bottom of their dives. Another interpretation is that as pups were making deeper dives with age, they were also spending increasingly more time near the bottom of each dive. Because females increase their foraging effort late in lactation, these changes in behavior may have been associated with pups following their mothers to deeper foraging areas.

The proportion of time that nursing bearded (*n = 4*) and ring seals (*n = 3*) spent in diving and hauled-out were not correlated with mass gain (Lydersen *et al*. 1994, Lydersen and Hammill 1993); however, sample size may have confounded those interpretations. In the current study, pups that spent a greater proportion of their activity budget in water also gained weight faster. At first, this correlation doesn't seem intuitive since swimming pups are likely to expend more energy than pups that remain hauled out and mostly sleep. One possibility is that faster growing pups have more surplus energy which affects their activity level. As another explanation, the energy expenditure of increased activity on the part of the pup may be compensated by the benefits of increased nursing opportunity by maintaining close proximity with the female. Alternatively, if the

female is large and healthy, she may choose to spend more time swimming with her pup

since she is less burdened by the need to forage. Larger females also have greater

reserves to be used for production of milk which would be reflected in faster pup growth.

The cause and effect of this relationship is uncertain but in the two later cases, pup

growth can be considered an index of female attendance. As previously mentioned,

females may motivate their pups to enter the water and dive; therefore, increased

attendance would explain both increased pup growth and proportion of time spent in

water. This explanation for the relationship between activity and growth may also help

explain the positive association between mass gain rate and mean dive duration. Higher

attendance would suggest that a larger proportion of pup dives were influenced by the

female's presence. Deeper diving for pups while they are being attended is consistent

with previously reported female-pup interactions since females remain submerged longer

than their pups and likely motivate them to lengthen their underwater stay (Bowen *et al*.

1999, Sato *et al.* 2003).

Once weaned, pups have been shown to use the deeper areas within their home

range which are likely preferred locations for foraging (Bjorge *et al.* 2002). As measured

in terms of weaned pup survival, there may be a multiplicative effect of female size and

condition on her fitness. First, larger females tend to have larger (Ellis *et al*. 2000) faster

growing pups and possess increased reserves allowing them to initially dedicate more

time to nursing their pups prior to foraging (Bowen *et al*. 1992, Thompson *et al*. 1994).

This can directly benefit the pup since increased size inherently allows it to dive longer

and increased reserves grants it more time after weaning to become self sufficient.

Second, increased size, may allow a female to impart more experience to her pup during

the lactation period. Increased time spent encouraging the pups to dive early in lactation

may increase the rate at which diving ability improves. By the time the female begins

foraging, the pup may be capable of following on some or all of her foraging trips. In

contrast, a smaller female would be forced to leave her less capable pup early in lactation.

This potential dichotomy in female behavior may best be illustrated by comparing pup

No. 2004-40, which grew at 0.58 kg/d, had the largest home range, spent 74% of the time

in water and 50% of the time diving, with Pup No. 2005-11 which exhibited lower

growth (0.29 kg/d), had a far smaller home range, spent 44% of the time in water and

only 27% of the time diving during a similar age interval (Table 2.2 and Table 2.3).

Ringed seals spend greater proportions of time diving with increasing age but data

from this study offers no evidence that there is a similar trend for harbor seal pups.

Although no significant factors were found to influence the proportion of time spent in

dives, individual diving behavior was highly variable (mean = 0.39, range: 0.19 - 0.60)

which suggests that other factors, which I did not incorporate in my analyses, are

involved. Dive frequency was influenced by both birth mass and mean depth available.

Similar to nursing Weddell seal pups (Burns 1999), dive frequency for harbor seal pups

tended to decrease with pup size. This is likely due to larger animals having a greater

ADL and therefore returning to the surface less often for air. This is also apparent from

mean and maximum dive duration, which tended to be longer for the larger pups included

in the current study. Although not previously shown for nursing phocids pups, Galapagos

fur seal pups, *Arctocephalus galapagoensis,* were found to have size related differences

in dive duration during the typically two year nursing period (Horning and Trillmich

1997). Similarly, dive duration of juvenile Weddell seals has been shown to be positively

influenced by body mass as a result of physiological influence of size on ADL (Burns 1999).

Post-dive surface intervals decreased with age as pups became more efficient swimmers. Increased swimming proficiency is likely to reduce the pup's overall diving oxygen consumption. Likewise, improved strategies for retrieving air during surfacing events would reduce the energetic costs associated with increased drag at the ocean surface (Williams and Kooyman 1985). Despite making longer dives, improvements in physiological training, swimming skills, and dive response were likely reducing the pup's overall dive metabolism with age and therefore reducing the time required to ventilate following dives. The mean depth available in their designated home range appeared to influence pup dive frequency and mean post-dive surface time. In deeper water, commuting time would be greater if females or pups were directing their dives to the ocean floor. It is conceivable that pups would spend more time waiting for their mother after returning to the surface for air if females were seeking the ocean floor. But this would not be consistent with previous accounts that showed pups increasing their dive frequency to maintain contact with their longer diving mother (Bowen *et al.* 1999).

Transit rate describes average swimming speed when traveling underwater to and from the bottom of a dive. By 15 dpp, maximum pup swimming speeds reported by Jorgensen *et al.* (2001) were 1.5 m/s, which is comparable to the maximum transit rate of 1.6 m/s seen for pups of the same age in this study. Despite the fact that harbor seal pups have been previously reported to increase maximum swimming speed over the entire duration of lactation (Jorgensen *et al.* 2001), mean and maximum transit rates only appeared to significantly increase between 0-5 dpp and 6-10 dpp in this study. It is

therefore likely that important swimming skills were developing early in lactation rather than over the entire nursing period.

Pups were likely using the bathymetry available to them based on the significant influence of depth available and tide height on pup behavior. This is implied by the indirect influence of mean depth available on dive frequency and post-dive surface interval, but also is shown by the direct effect of available depth on mean diving depth. On average, pups dove deeper during high tide cycles and as maximum depth available increased ($r^2 = 0.23$). The significance of maximum versus mean depth available on diving depth suggests that female-pup pairs were not only using the available bathymetry but were seeking deeper areas within their home range. This would be consistent with expected adult foraging behavior (Eguchi and Harvey 2005).

Bathymetric constraints on diving depth may explain why age alone was not significant in explaining changes in mean or maximum diving depth in the ANOVA analysis. Large between-subject variance was likely caused by differences in sea-floor topography near natal haul outs. Similarly, nearby ocean topography may have explained differences in the maximum dives of nursing ringed seal pups (Lydersen and Hammill 1993). I observed a weak influence of age on mean diving depth after controlling for tide height; however, water depths increased with distance from haul out ledges and female-pups were observed diving farther from natal haul out sites as pups aged. Thus, age related changes in diving behavior may have resulted from shifts in the spatial distribution of dives. This is also suggested by changes in the relationship between maximum depths achieved and the maximum depth available across age groups (Figure 2.8). In the first half of lactation, there was a strong correlation between dive depth and

bathymetry within 2 km of observed locations. Pup were later making undetected trips to deeper water (Table 2.6) and the observed correlation between dive depth and bathymetry became weak (Figure 2.8B).

The maximum depth to which a pup can dive is theoretically constrained by its ability to breath-hold and the speed at which it can transit vertically in the water column. At birth, pups swim up to 1 m/s (Jorgensen *et al*. 2001) and hold their breath for about 1 minute (Bowen *et al.* 1999). By these estimates, newborns should be capable of reaching depths of around 30 m. Bathymetry adjacent to their haul out sites in this study area was often less than 30 m and became extremely shallow near pupping ledges. From birth to 5 dpp, the depth available within 2 km likely overestimated depths available to pups as they remained close to haul outs, resulting in a slope of less than 1 for the coefficient describing the relationship between diving depths and depths available (Figure 2.8A). By 5 dpp, pups were reaching deeper water near the edge of the home range and achieved dives up to 32 m (Pup No. 2005-23). By 10 dpp Pup No. 2004-40 made a dive of 65 m which is considerably deeper than maximum dives reported for nursing pups 0-19 dpp on Sable Island (35m, Bowen *et al*. 1999), 0-42 dpp in the St. Lawrence River Estuary (30.9m, Greaves *et al.* 2005), and pups 0-21 dpp studied in Svalbard (30m, Jorgensen *et al*. 2001). At ages 19 and 26 dpp, two potentially weaned pups (Pup No. 2005-58 and 2005-62) achieved depths of about 100 m during dives lasting 3min 16sec. These dives were deeper than values reported for harbor seal pups in other studies (Bowen *et al*. 1999, Jorgensen *et al.* 2001, Greaves *et al.* 2005) as well as for bearded (86m, Lydersen *et al*. 1994) and ringed seal pups (89m, Lydersen and Hammill 1993). To achieve these depths these pups would have had to travel approximately about 13 km outside of their

designated home range. It is most likely that these pups were following their mother or other seals to these deeper sites since they are relatively few and distant from their normal haul-out locations and would not have been likely found by random chance (see areas labeled as '90m' in Figure 2.1).

A potential weakness in this study resulted from an inability to locate pups as they left the study area late in lactation (Table 2.6). Pups were not relocated daily during the deployment period and in part due to the limited range of the VHF transmitters used (~4-6km) older pups were not found for days at a time. The home ranges I defined, therefore, did not reflect the actual areas used by pups late in lactation (Figure 2.8B) but were still useful in comparing maximum dive depths to depths available in younger pups. Furthermore, this approach is conservative since inaccurately designated home ranges would only tend to reduce the significant relationship between pup behavior and depth available.

Because the TDR data used in this study was relatively low resolution (14-28s in this study versus 1-10s in other research), surfacing events occurring between records could have been potentially missed. This would result in an overestimation of dive duration. Missed surfacing events did not appear to be a problem in this study since the maximum observed dive duration of 4.7 min in this study was shorter than the maximum reported for pups on Sable Island (9.2 min, Bowen *et al*. 1999) and in the St. Lawrence River Estuary (5.9 min, Greaves *et al.* 2005) and only slightly longer than observed in Norway (3.7 min, Jorgensen *et al.* 2001).

In order to better understand what influences the diving tendencies of nursing pups, it is important to model the entire suite of motivators and constraints affecting

behavior. There are several approaches I took in this study which might be considered in future research. First, in this study I used an index of bathymetry when modeling variations in nursing pup activity and dive performance. Maximum depths available were highly correlated with maximum dive duration, maximum dive depth, and mean dive frequency. The importance of bathymetry in these models of maximal dive metrics suggests that they should be considered before using these measures to describe the "ability" of nursing pups. Secondly, I modeled behavior using the individual pup as the unit of observation. Although previous studies have used this approach to describe mean dive behavior (Burns 1999), most researchers have included multiple ages of each animal in their models. Care must be taken to ensure a properly balanced statistical design is achieved and pseudo-replication is avoided when ages are often staggered and the length of deployment varies between individuals. Here I've shown that these difficulties can be successfully overcome by averaging behavior over an entire deployment period. Surprisingly, this method still detected an age effect and there was no significant effect of deployment length, which varied considerably between individuals. Furthermore, this method was able to detect an effect of age on the amount of time pups spent in water during lactation. This effect was otherwise non-significant when examined using a one-way ANOVA between age groups, therefore, emphasizing the need to control for environmental factors such as tide height when studying diving development.

Conclusions – Harbor seal pup diving behavior changes throughout the lactation period. During the first week, development is likely related to improvements in diving techniques and swimming skills, since the observed changes in behavior are drastic compared to

improvements in pup diving physiology. In the later part of lactation, increased activity, dive depth and duration, are likely influenced by bathymetry and changes in pup motivation. Although studies of neonate diving behavior have become popular in recent years, there has been little attempt to relate observed behavior to the potential constraints of bathymetry. This study emphasizes the importance of considering depth available when attempting to interpret neonate diving behavior. Furthermore, there is circumstantial evidence from this study and previous work (Bowen *et al.* 1999) that harbor seal females lead their pups into dives and potentially motivate them to dive deeper and longer than they would otherwise attempt alone. Female size may play an important role in the development of harbor seal pup diving ability, since larger females potentially spend more time actively swimming and diving with their pup. Highly attended pups are likely to be weaned with improved diving skills and a broader range of experience. Further study is needed to determine whether the combined effects of diving experience and fat accumulation at the time of weaning influences pup survival – a more biologically significant outcome in terms of understanding the relationship between an individual female's maternal investment strategy and its affect on her reproductive fitness.

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APPENDICES

APPENDIX A

Data Used for Analysis of Factors Affecting Mass Gain Rate

Table A.1. Data for 30 non-lanugo, nursing pups used in AIC model selection analysis to determine the factors influencing pup mass gain rate during lactation.

Year and Pup No.	Sex	Initial Capture Date	Age Interval (dpp)	Initial Length (cm)	Mass Gain Rate (kg/d)	Movement[a] (m/d)	Activity[b] (percent)	Attendance[c] (percent)	Max. Depth Available	Relocations	
										Visual	All[d]
2004-04	M	May 13	1 - 9	79	0.13	60	11	67	26	3	9
2004-05	F	May 13	3 - 11	81	0.79	61	60	33	28	3	10
2004-06	F	May 14	3 - 16	89	0.67	90	33	100	62	6	12
2004-10	F	May 19	3 - 15	84	0.68	1438	50	83	42	6	14
2004-13	M	May 20	1 - 2	75	0.60	644	83	67	28	3	6
2004-17	M	May 21	3 - 13	76	0.50	355	45	100	31	4	11
2004-37	M	Jun 01	5 - 16	82	0.61	349	63	100	62	5	16
2005-01	M	May 04	1 - 7	81	0.10	60	40	100	30	5	5
2005-05	M	May 08	3 - 12	82	0.38	339	27	44	23	9	15
2005-07	M	May 13	2 - 19	79	0.54	675	46	50	62	4	13
2005-09	F	May 13	1 - 14	77	0.51	429	88	83	31	6	16
2005-11	F	May 15	4 - 15	72	0.29	41	31	100	31	4	13
2005-12	M	May 15	1 - 16	79	0.29	132	54	100	62	8	26
2005-13	M	May 15	1 - 6	75	0.32	80	14	100	62	6	14
2005-15	M	May 16	4 - 19	73	0.36	1770	47	75	43	8	17

[a] Movement is the sum of the distance between all relocations divided by the number of days between captures.
[b] Activity is the proportion of observation that the pup was in water (versus hauled out).
[c] Attendance is the proportion of visual observations when female was present with pup.
[d] The sum of visual and VHF radio signal relocations.

Table A.1. Continued.

Year and Pup No.	Sex	Initial Capture Date	Age Interval *(dpp)*	Initial Length *(cm)*	Mass Gain Rate *(kg/d)*	Movement [a] *(m/d)*	Activity [b] *(percent)*	Attendance [c] *(percent)*	Max. Depth Available	Relocations Visual	All [d]
2005-17	M	May 16	1 - 11	82	0.57	1269	38	100	62	4	13
2005-18	M	May 17	3 - 16	81	0.48	125	41	100	23	3	17
2005-20	M	May 18	2 - 13	77	0.55	110	71	100	30	4	7
2005-21	M	May 17	3 - 15	81	0.17	528	40	100	28	5	15
2005-22	F	May 17	1 - 14	72	0.62	270	75	75	62	4	12
2005-23	F	May 19	1 - 13	83	0.63	523	85	100	97	3	13
2005-24	F	May 19	3 - 15	79	0.42	61	74	100	62	7	19
2005-25	M	May 20	2 - 8	83	0.63	59	40	67	62	3	5
2005-26	M	May 18	4 - 13	73	0.47	239	73	67	32	3	11
2005-28	M	May 19	2 - 14	76	0.22	52	33	100	62	5	18
2005-29	M	May 26	3 - 9	85	0.40	89	36	75	26	4	14
2005-36	F	May 27	4 - 17	77	0.37	602	58	83	33	6	19
2005-40	F	May 28	2 - 23	80	0.30	32	36	86	62	7	14
2005-53	F	Jun 03	8 - 13	86	0.60	3088	78	60	32	5	9
2005-56	M	Jun 04	9 - 24	83	0.09	118	71	57	31	7	21

[a] Movement is the sum of the distance between all relocations divided by the number of days between captures.
[b] Activity is the proportion of observation that the pup was in water (versus hauled out).
[c] Attendance is the proportion of visual observations when female was present with pup.
[d] The sum of visual and VHF radio signal relocations.

APPENDIX B

Pup Age Prediction Model: Selection Using AIC

Table B.1. The list of candidate generalized linear models (GLM) for predicting pup ages in 2004 sorted by increasing AICc value. Model #15 had the lowest model AICc value and was considered the best model. Model #0 was the global candidate model.

Model	Model Parameters [a]	K	n	R^2_{adj}	SSE	Outliers[b] r_i	Outliers[b] h	AIC	AIC_c	ΔAIC_c	w_i
15	**G + N**	4	39	0.66	1.91	0	3	-109.7	-108.5	0.00	0.45
17	$G + G^2 + N$	5	39	0.66	1.89	0	4	-108.1	-106.3	2.17	0.15
6	G + S + N + G*N	6	39	0.67	1.79	0	13	-108.2	-105.5	2.96	0.10
5	$G + G^2 + N + G*N$	6	39	0.67	1.79	0	13	-108.1	-105.5	2.98	0.10
10	G + S + N + G*S	6	39	0.65	1.86	0	7	-106.7	-104.1	4.37	0.05
12	$G + G^2 + S + N$	6	39	0.65	1.88	0	4	-106.2	-103.6	4.87	0.04
13	G + S + N	6	39	0.66	1.90	0	2	-105.9	-103.3	5.20	0.03
4	$G + G^2 + S + N + G*N$	7	39	0.66	1.78	0	13	-106.4	-102.8	5.73	0.03
7	G + S + N + G*S + G*N	7	39	0.66	1.79	0	20	-106.3	-102.6	5.84	0.02
3	$G + G^2 + S + N + G*S$	7	39	0.65	1.84	0	7	-105.2	-101.6	6.89	0.01
2	$G + G^2 + S + N + G*S + G*N$	8	39	0.65	1.77	0	17	-104.5	-99.7	8.76	0.01
8	G + S + N + G*S + G*N + G*S*N	8	39	0.65	1.79	1	26	-104.3	-99.5	9.03	0.00
0	$G + G^2 + S + N + G*S + G*N + G*S*N$	9	39	0.64	1.77	1	26	-102.6	-96.4	12.13	0.00
19	G	3	39	0.48	3.02	1	2	-93.8	-93.1	15.35	0.00
14	G + S	4	39	0.47	2.99	1	1	-92.2	-91.0	17.50	0.00
18	$G + G^2$	4	39	0.47	3.02	1	4	-91.8	-90.7	17.82	0.00
11	G + S + G*S	5	39	0.46	2.97	1	6	-90.4	-88.6	19.93	0.00
16	$G + G^2 + S$	5	39	0.46	2.99	1	4	-90.2	-88.3	20.14	0.00
9	$G + G^2 + S + G*S$	6	39	0.45	2.97	1	6	-88.4	-85.7	22.74	0.00
20	N	3	41	0.25	4.94	0	0	-80.7	-80.1	28.40	0.00
1	CONSTANT	2	41	0.00	6.73	0	41	-70.1	-69.8	38.68	0.00
21	S	3	41	0.00	6.54	0	0	-69.3	-68.6	39.87	0.00

[a] Parameters used included mean upper canine tooth length (Cm), axillary girth (G), nursing status (N), and sex (S).
[b] Observations with large studentized residuals ($r_i > 3.5$) or high leverage ($h > 0.10$) were counted as outliers.

Table B.2. The list of candidate generalized linear models (GLM) for predicting pup ages in 2005 sorted by increasing AICc value. Model #35 had the lowest model AICc value and was considered the best model. Model #0 was the candidate global model.

Model	Model Parameters [a]	K	n	R^2_{adj}	SSE	Outliers[b] r_i	Outliers[b] h	AIC	AIC$_c$	ΔAIC$_c$	w_i
35	Cm + G + N	5	66	0.86	706.5	0	1	166.5	167.5	0.00	0.24
26	Cm + G + S + N + G*N	7	66	0.87	662.2	0	8	166.2	168.1	0.66	0.17
30	Cm + G + S + N + G*S	7	66	0.86	673.5	0	4	167.3	169.2	1.77	0.10
27	Cm + G + S + N + G*S + G*N	8	66	0.87	647.7	0	9	166.7	169.3	1.79	0.10
37	Cm + G + G^2 + N	6	66	0.86	704.3	0	8	168.3	169.7	2.21	0.08
25	Cm + G + G^2 + N + G*N	7	66	0.86	680.9	0	9	168.0	170.0	2.50	0.07
24	Cm + G + G^2 + S + N + G*N	8	66	0.86	662.1	0	9	168.2	170.7	3.24	0.05
32	Cm + G + G^2 + S + N	7	66	0.86	690.9	0	8	169.0	170.9	3.45	0.04
33	Cm + G + S + N	7	66	0.86	692.3	0	1	169.1	171.1	3.59	0.04
23	Cm + G + G^2 + S + N + G*S	8	66	0.86	669.4	0	10	168.9	171.4	3.96	0.03
28	Cm + G + S + N + G*S + G*N + G*S*N	9	66	0.86	646.4	0	12	168.6	171.8	4.35	0.03
22	Cm + G + G^2 + S + N + G*S + G*N	9	66	0.86	647.5	0	10	168.7	171.9	4.45	0.03
0	Cm + G + G^2 + S + N + G*S + G*N + G*S*N	10	66	0.86	646.1	0	13	170.6	174.6	7.10	0.01
6	G + S + N + G*N	6	68	0.86	733.9	0	6	173.8	175.1	7.67	0.01
7	G + S + N + G*S + G*N	7	68	0.86	726.7	0	8	175.1	177.0	9.49	0.00
15	G + N	4	68	0.85	808.4	0	3	176.3	177.0	9.51	0.00
4	G + G^2 + S + N + G*N	7	68	0.85	733.9	0	7	175.8	177.6	10.16	0.00
5	G + G^2 + N + G*N	6	68	0.85	765.2	0	8	176.6	178.0	10.52	0.00
10	G + S + N + G*S	6	68	0.85	772.6	0	5	177.3	178.6	11.17	0.00
17	G + G^2 + N	5	68	0.85	801.6	0	7	177.8	178.7	11.27	0.00
12	G + G^2 + S + N	6	68	0.85	778.7	0	7	177.8	179.2	11.70	0.00
8	G + S + N + G*S + G*N + G*S*N	8	68	0.85	724.1	0	14	176.9	179.3	11.83	0.00

[a] Parameters used included mean upper canine tooth length (Cm), axillary girth (G), nursing status (N), and sex (S).
[b] Observations with large studentized residuals (r_i >3.5) or high leverage (h > 0.10) were counted as outliers.

Table B.2. Continued.

Model	Model Parameters [a]	K	n	R^2_{adj}	SSE	Outliers [b] r_i	h	AIC	AIC_c	ΔAIC_c	w_i
2	$G + G^2 + S + N + G*S + G*N$	8	68	0.85	726.3	0	10	177.1	179.5	12.03	0.00
13	$G + S + N$	6	68	0.85	783.3	0	1	178.2	179.6	12.11	0.00
3	$G + G^2 + S + N + G*S$	7	68	0.85	764.7	0	9	178.6	180.4	12.96	0.00
38	$Cm + G + G^2$	5	66	0.79	1045.6	0	6	192.3	193.3	25.87	0.00
36	$Cm + G + G^2 + S$	6	66	0.80	1013.0	0	5	192.2	193.7	26.20	0.00
29	$Cm + G + G^2 + S + G*S$	7	66	0.80	994.8	0	8	193.1	195.0	27.52	0.00
34	$Cm + G + S$	5	66	0.79	1084.0	0	0	194.7	195.7	28.25	0.00
39	$Cm + G$	4	66	0.78	1131.1	0	0	195.5	196.2	28.71	0.00
31	$Cm + G + S + G*S$	6	66	0.78	1077.9	0	3	199.9	201.3	33.81	0.00
16	$G + G^2 + S$	5	68	0.77	1212.6	0	6	205.9	206.9	39.41	0.00
18	$G + G^2$	4	68	0.76	1272.7	0	7	207.2	207.8	40.37	0.00
9	$G + G^2 + S + G*S$	6	68	0.76	1204.0	0	8	207.4	208.8	41.33	0.00
14	$G + S$	4	68	0.74	1348.4	0	1	211.1	211.8	44.29	0.00
11	$G + S + G*S$	5	68	0.74	1348.3	0	3	213.1	214.1	46.62	0.00
19	G	3	68	0.73	1444.3	0	2	213.8	214.2	46.71	0.00
40	$Cm + N$	4	66	0.58	2189.7	0	1	239.1	239.8	72.31	0.00
42	Cm	3	66	0.47	2792.0	0	0	253.2	253.5	86.08	0.00
41	$Cm + S$	4	66	0.46	2791.8	0	0	255.2	255.8	88.35	0.00
20	N	3	70	0.25	4065.8	0	0	290.3	290.7	123.2	0.00
1	CONSTANT	2	70	0.00	5510.6	0	70	309.6	309.8	142.3	0.00

[a] Parameters used included mean upper canine tooth length (Cm), axillary girth (G), nursing status (N), and sex (S).
[b] Observations with large studentized residuals ($r_i > 3.5$) or high leverage ($h > 0.10$) were counted as outliers.

APPENDIX C

Time-Depth Recorder Assembly: Construction and Attachment Diagram
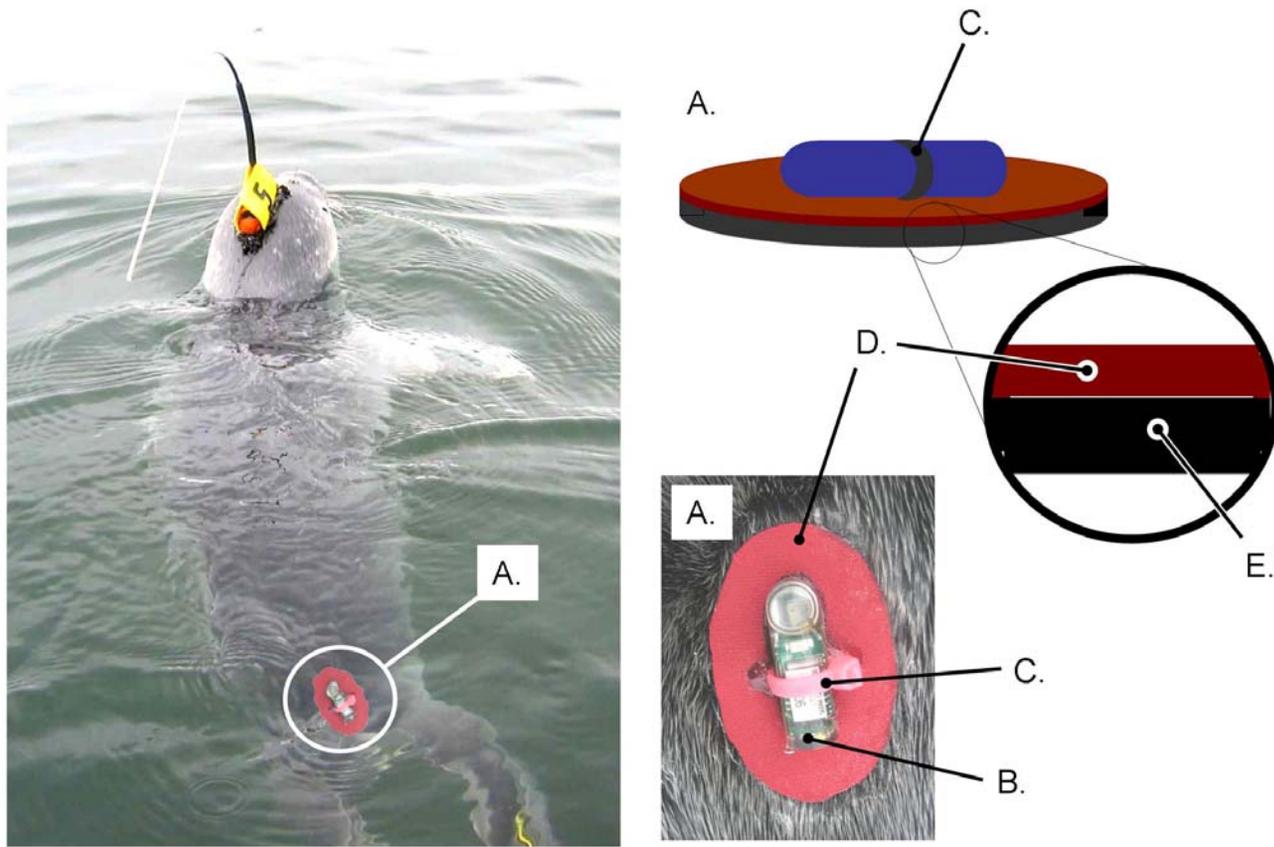
Figure C.1. A photo and schematic showing the attachment location and construction of the time-depth recorder assembly (A). Each assembly consisted of a LTD-1100 or LTD-1110 TDR (B.) glued and secured with a cable tie (C.) to the cloth surface (D.) of a bi-layered neoprene material (D., E.). The neoprene rubber surface (E.) was glued to the fur of the pup. The assembly was attached to the fur on the lower back about 3-5 inches above the tail.

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John Peter Skinner was born in San Francisco, California on 18 January 1973. He was raised in the small, agricultural town of Petaluma and graduated from Petaluma High School in 1991. Following high school, John volunteered for a six year tour in the United States Navy serving aboard the USS William H. Bates (SSN 637) -- a nuclear submarine stationed out of Honolulu, Hawaii. Upon receiving an honorable discharge he turned his interest to wildlife. He pursued a Bachelor of Science degree in Wildlife Biology at Colorado State University from 1998 to 2001 and graduated as *cum laude* with the first class of the new millennium in May 2001. During the remainder of 2001, John assisted with research examining mule deer fawn survivorship on the Uncompahgre Plateau in Colorado for the Colorado Division of Wildlife (CDOW). He then served as a field assistant for the Cooperative Allegheny Bear Study with Virginia Polytechnic Institute in the winter of 2001/2002 and then returned to Colorado to work for the National Park Service examining peregrine falcon eyrie success in Dinosaur National Monument. In 2002/2003, John again worked as a seasonal employee for the CDOW studying mule deer population dynamics in Middle Park, Colorado. John began a graduate program in the Department of Wildlife Ecology at the University of Maine in September 2003 and is a candidate for the Master of Science degree in Wildlife Ecology from the University of Maine in August 2006.