Growth and reproductive tracts from fetal to adult harbor seals in the Gulf of Alaska

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ABSTRACT: Harbor seals *Phoca vitulina* in Alaska have experienced large fluctuations in abundance in recent decades. Changes in environmental conditions can significantly influence growth and reproductive characteristics of individuals, potentially leading to changes in population size. This study assesses pre- and postnatal growth and sexual maturity of harbor seals in the Gulf of Alaska using samples collected by subsistence hunters as part of the Alaska Native Harbor Seal Commission's Biosampling Program from 1998 through 2005. Female harbor seals matured at a minimum age of 3 yr, standard length of 122 cm, and mass of 48 kg. The average age of sexual maturity was 4.2 ± 0.7 yr (95% CI). Female seals attained an asymptotic standard length of 147.7 ± 2.6 cm and body mass of 82.2 ± 4.8 kg. Fetuses increased 0.33 cm d^{-1} standard length and 0.09 g$^{1/3}$ d^{-1} mass. Implantation date ranged from 22 September to 17 October, with a mean ± SD date of 30 September ± 8 d. Age at onset of reproduction portends improvements in reproductive rates and possibly environmental conditions since the population crash in the late 1970s. Harbor seals in the present study are smaller in length and have later implantation dates with lower pregnancy rates than in the 1960s. These indices may reflect that environmental conditions are not currently at optimal levels and are limiting growth and maturation.

KEY WORDS: Harbor seal · Sexual maturity · Fetal growth · Alaska · Subsistence

INTRODUCTION

Life history characteristics such as growth, survival, and reproduction are influenced by population density and environmental conditions. Population density plays a crucial role in determining the reproductive characteristics in mammals (Fowler 1987, 1990, Wauters & Lens 1995, Bonenfant et al. 2002, Williams et al. 2013). As population density increases, or environmental constraints become more limiting, organisms must make trade-offs between survival, growth, and reproduction (Stearns 1989). When resources are limited, the body mass of individuals typically declines and animals often reduce the amount of energy allocated to reproduction, increasing the age of first reproduction and reducing

reproductive success (Scheffer 1955, Bengtson & Laws 1985, Fowler 1990, Wauters & Lens 1995, Festa-Bianchet & Jorgenson 1998, Williams et al. 2013). Density-dependent theory predicts that for populations in which declines are driven by bottom-up causes, such as resource limitation, one expects to see slow growth and delayed mean age of sexual maturity (Stearns 1976). In populations driven by top-down influences, such as predation, one expects to see rapid growth and early maturity (Stearns 1976). Consequently, understanding growth and reproduction of marine mammal populations is not only important for management, but can also provide insight into population density and/or prey availability, including changes over time and space.

Harbor seals *Phoca vitulina* in Alaska have experienced large fluctuations in population size and density in recent decades. At Tugidak Island (central Gulf of Alaska), the population of harbor seals declined by an estimated 85% between 1976 and 1988 (Pitcher 1990). In Prince William Sound, abundance declined by approximately 63% between 1984 and 1997 (Frost et al. 1999). Aialik Bay, a tidewater glacial fjord, also experienced large declines beginning in the early 1980s (Hoover-Miller et al. 2011). The populations of harbor seals at Tugidak Island, Prince William Sound, and Aialik Bay have stabilized since the mid-1990s and early 2000s, and all show indications of increasing trends (Jemison et al. 2006, Hoover-Miller et al. 2011, Allen & Angliss 2013). Harbor seals in areas of Southeast Alaska, such as Ketchikan and Sitka, have been stable or increasing (Small et al. 2003). However, in Glacier Bay, harbor seals declined by up to 75% from 1992 to 2002 and they have continued to decline since then (Hoover-Miller 1994, Mathews & Pendleton 2006, Womble et al. 2010). The broad-scale nature of the declines and stabilization or recovery in many areas suggests large-scale environmental change may have contributed to the declines.

What exactly caused these harbor seal declines, and why Glacier Bay continues to decline at an alarming rate despite ecological and anthropogenic protections is largely unknown (Mathews & Pendleton 2006, Womble et al. 2010). These changes in population density, in conjunction with environmental fluctuations, can produce profound changes in individual growth and reproductive characteristics, including timing of mating and birth (Hood & Ono 1997, Laidre et al. 2006, Holmes et al. 2007).

The timing of harbor seal breeding and birthing varies geographically, but is highly synchronized within a particular region (Bigg 1969a, Temte et al. 1991, Temte 1994). In the Gulf of Alaska (GOA), pups are born from May through mid-July (Pitcher & Calkins 1979, Jemison & Kelly 2001). After birth, the mother nurses her pup for approximately 4 to 6 wk (Bigg 1969b, Bigg & Fisher 1974, Pitcher & Calkins 1979). Female harbor seals come into estrus and mate shortly after weaning (Bigg & Fisher 1974, Pitcher & Calkins 1979). The development of the embryo is suspended at the blastocyst stage for approximately 1.5 to 3.0 mo, in a process referred to as embryonic diapause, ensuring that pups are born when environmental conditions are most favorable to their survival (Fisher 1954, Bishop 1967, Bigg 1969b, Bigg & Fisher 1974, Pitcher & Calkins 1979, Boyd 1991, Atkinson 1997). Following embryonic diapause, the blastocyst attaches to the uterine wall and continues to develop

for 8 to 9 mo of active fetal development, also referred to as placental gestation (Bigg & Fisher 1974, Boyd 1991).

The data and samples utilized for the present research came from wild and presumed healthy harbor seals harvested for subsistence purposes by Alaska natives and collected by the Alaska Native Harbor Seal Commission (ANHSC)'s Biosampling Program. In the past, reproduction in marine mammals was traditionally studied using lethal methods and gross macroscopic and microscopic examinations of the reproductive tracts. Collecting biological samples from marine mammals became much more challenging after the enactment of the Marine Mammal Protection Act (MMPA) in 1972 (16 USC Chapter 31). The MMPA established federal control over marine mammal management in the USA and prohibited all takes of marine mammals. Section 1378 of that chapter provides an exemption for Alaska natives for non-wasteful subsistence harvests for food and traditional native handicrafts. The ANHSC's Biosampling Program provides tissues from subsistence harvests for scientific research. Biosamples from subsistence-harvested animals provides tissues and associated data necessary to assess the health and condition of seals, without the need to sacrifice individuals strictly for scientific purposes and abides by current MMPA regulations.

This study investigates female growth, reproductive biology, and fetal growth of harbor seals from the GOA. We used morphometric measurements and reproductive tracts collected from subsistence-harvested animals to (1) examine both prenatal and postnatal growth and (2) characterize sexual maturity as a function of age and body size. Understanding the growth and reproductive characteristics of harbor seal populations in Alaska, in light of the population fluctuations over recent decades, is crucial for understanding past and future life history characteristics.

MATERIALS AND METHODS

Study area and animals

Between 1996 and 2006 the ANHSC's Biosampling Program trained and certified 155 biosampling technicians from 40 native villages on standardized scientific protocols for the collection of morphometric measurements and tissue samples from subsistence-harvested harbor seals. Samples and associated metadata are managed by the University of Alaska Museum of the North. A subset of those samples were used in this research, including reproductive
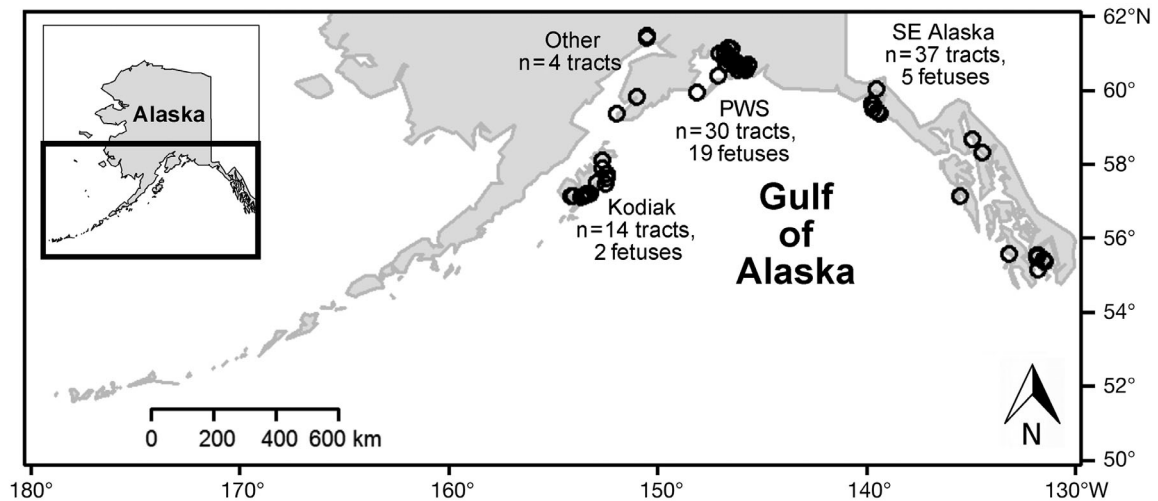
Fig. 1. Locations of subsistence-harvested harbor seals used in this study. Female harbor seals were harvested by Alaska native subsistence hunters from 1998 to 2005 as part of the Alaska Native Harbor Seal Commission's Biosampling Program. Eighty-five reproductive tracts and 27 fetuses were collected from Southeast Alaska, Prince William Sound (PWS), Kodiak, and the Kenai Peninsula area. One fetus was from an unknown region of the Gulf of Alaska

tracts from 85 female harbor seals and 27 fetuses collected between 1998 and 2005 throughout the GOA (Fig. 1). Sample sizes in some comparisons may be smaller due to incomplete measurements or tissue collections for some seals. In the field, each female reproductive tract, including the uterus and both ovaries, was removed in its entirety. If the seal was pregnant and a fetus was present, the fetus typically was left in the uterus, although near-term fetuses were removed from the uterus. The entire reproductive tract was placed in a Ziploc bag and frozen before being shipped for analysis. In addition to the reproductive tract, the biosample technician collected data on date, location, body mass, standard length, evidence of lactation, and any abnormalities of the harvested seal. Body mass was measured to the nearest pound using a hanging scale. Standard length was measured to the nearest cm from the tip of the nose to the tip of the tail along a flat surface with the seal on its back. Either a canine or post canine tooth was collected from each seal and sent to Matson's Laboratory in Missoula, Montana for aging (Blundell & Pendleton 2008).

Laboratory analyses

Each reproductive tract was thawed before examination in the laboratory. The right and left ovaries were separated from the reproductive tracts and the length, width, and depth of each ovary were measured to the nearest 0.1 cm. The ovaries were 'butterflied'

by bisecting and longitudinally examined under a dissecting microscope for evidence of corpora lutea and corpora albicantia. The number of corpora lutea and corpora albicantia in each ovary were counted and recorded and then combined for both ovaries.

After being excised from the uterine horn, each fetus was weighed and the sex determined. The mass of the fetus was measured to the nearest g. Standard length, curvilinear length, and axillary girth were all measured to the nearest 0.1 cm. Standard length was measured identically to that of older seals. Curvilinear length was measured from the tip of the nose to the tip of the tail following the curve of the body, and axillary girth was measured around the body of the fetus just under the pectoral flippers. On each fetal skull, 4 cranial measurements were taken to the nearest 0.1 cm. These measurements included (1) the skull length from the back of the skull to the anterior extent of the zygomatic process, (2) the condylobasal length (CBL) from the tip of the nose to the back of the skull, (3) the maximum skull width measured at the base of the skull, and (4) the zygomatic width measured across the skull from the distal extent of the zygomatic process (Fig. 2).

Data analysis

Postnatal growth was described using von Bertalanffy growth curves (von Bertalanffy 1957, Lydersen & Kovacs 2005). Growth curves for standard length and body mass were of the form:
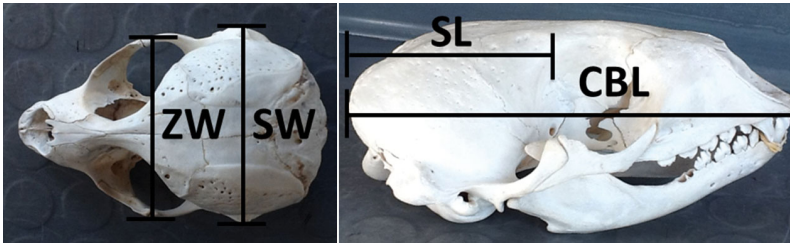
Fig. 2. The 4 cranial measurements taken on each harbor seal fetal skull: zygomatic width (ZW), maximum skull width (SW), skull length (SL), and condylobasal length (CBL). Photo credit: Kate Wynne

$$L_x \text{ (or } M_x) = L_\infty (\text{or } M_\infty)[1 - e^{-a(x-x_0)}]^b \qquad (1)$$

where L_∞ and M_∞ are the asymptotic length (cm) and mass (kg), L_x and M_x are the length and mass at time x, x is the age of the seal in years, x_0 is an estimated time before birth when the embryo begins to grow after embryonic diapause (McLaren 1993), e = 2.71828 (a mathematical constant that is the base of the natural logarithm), and a and b are both constants, where a describes the rate of approach to the horizontal asymptote and b describes the curvilinearity of that approach (McLaren 1993). A value of −0.63 yr was chosen for x_0 based on data for harbor seals in the GOA in McLaren (1993), and was also supported by our fetal data. Growth models were fit in R, version 3.0.2 (R Core Team 2013) using nonlinear least squares estimation.

An ANCOVA test was run to determine any significant differences between male and female fetuses for each fetal measurement. Fetal growth was described using linear regression analysis to examine standard length, curvilinear length, axillary girth, the cube root of mass, and the 4 skull measurements as a function of the day of the year the mother was harvested (Stewart et al. 1989, Garlich-Miller & Stewart 1999, Chabot & Stenson 2000, Yunker et al. 2005). Day 1 and Day 366 represent 1 January in consecutive years (Garlich-Miller & Stewart 1999, Chabot & Stenson 2000, Yunker et al. 2005). The day of implantation was approximated by the x-intercept of the inverse regression of day of the year on fetal growth (Stewart et al. 1989, Garlich-Miller & Stewart 1999, Chabot & Stenson 2000). The extrapolated estimates were then averaged to produce a mean implantation date.

Each seal was categorized as reproductively immature, non-pregnant, or pregnant to compare morphometric measurements by reproductive status. The onset of sexual maturity was defined as the age at which a female first ovulated. The average age of sexual maturity (ASM) was determined using the technique described by DeMaster (1978). Seals were considered immature if their ovaries showed no signs of prior ovulations and the uterus and uterine horns were noticeably small and had not previously expanded or experienced involution subsequent to a prior pregnancy. Females with ovaries that contained at least one corpus luteum or corpus albicantium were considered sexually mature. Non-pregnant seals were sexually mature seals that were not pregnant at the time of harvest. When analyzing the ovarian measurements, pregnant seal ovaries were further categorized as pregnant-active (ovary on the pregnant side of the reproductive tract) or pregnant-inactive (ovary on the non-pregnant side of the reproductive tract). For immature and non-pregnant animals, the mean volume of the right and left ovaries was recorded. Lactating animals (n = 2) were excluded from this analysis due to a small sample size and unique reproductive state that did not exactly fit into any of the aforementioned reproductive categories. Body mass and ovary volume data were log-transformed to achieve normality. Standard length, body mass, and ovary mass were then compared among reproductive statuses using ANOVA and post-hoc Tukey-Kramer multiple comparison tests. The significance level for all tests was $p \leq 0.05$. Pregnancy rates were calculated by age and compared with data reported by Bigg (1966) and Pitcher & Calkins (1979). As Pitcher & Calkins (1979) only used tracts collected after the embryonic diapause, we only used data from animals collected from a comparable time frame (i.e. excluding July–October data).

RESULTS

Postnatal growth

The age of animals used in the postnatal growth analysis ranged over 0–21 yr. Growth was asymptotic in both standard length and body mass. The von Bertalanffy growth model fitted the data well ($p < 0.05$; Fig. 3, Table 1). Seals attained an asymptotic standard length (mean ± SE) of 147.7 ± 2.6 cm and body mass of 82.2 ± 4.8 kg. The largest seal collected in this study was pregnant at the time of capture and was 13 yr old, weighed 104.4 kg, and measured 150 cm in length. The largest non-pregnant seal was 8 yr old, weighed 80.8 kg, and measured 159 cm in
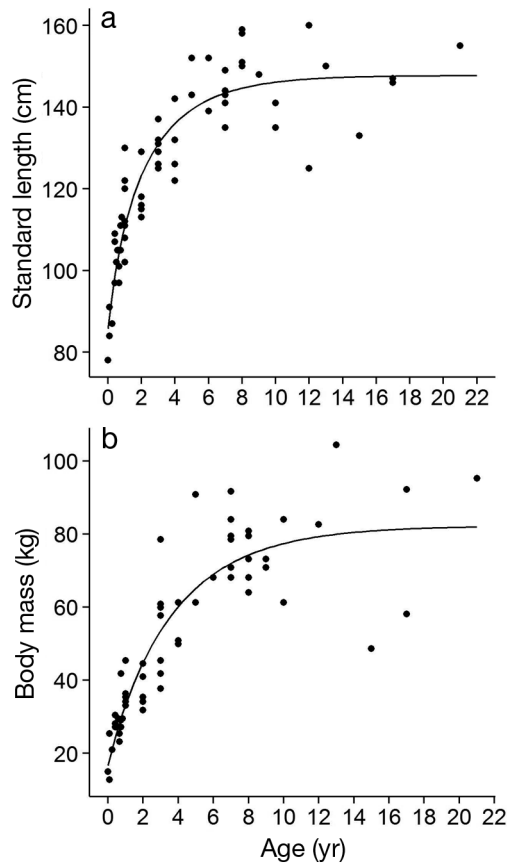
Fig. 3. von Bertalanffy growth curves fitted to (a) standard body length (n = 65) and (b) body mass (n = 63). See Table 1 for parameter values

the extensive off-loading of lipid resources that a mother seal provides to its pup through lactation.

Fetal growth

Of the 27 fetuses, 16 were male and 11 were female. Data from male and female fetuses were combined due to no significant difference between sexes for standard and curvilinear length, axillary girth, body mass and all 4 skull measurements (Table 2). All measurements were plotted as a function of day of the year (Figs. 4 & 5). Standard length ($r^2 = 0.95$, n = 27), curvilinear length ($r^2 = 0.92$, n = 25), axillary girth ($r^2 = 0.92$, n = 24), the cube root of body mass ($r^2 = 0.88$, n = 27), skull length ($r^2 = 0.76$, n = 26), CBL ($r^2 = 0.92$, n = 27), skull width ($r^2 = 0.95$, n = 27), and zygomatic width ($r^2 = 0.93$, n = 26) all showed a strong linear relationship with day of the year. Predicted growth rates are presented in Table 2. The x-intercept of the linear least-squares regression provided estimates of the implantation date for each measure. Those dates ranged from 22 September to 17 October, with a mean ± SE of 30 September ± 8 d.

Sexual maturity

Seal reproductive status had a statistically significant effect on both body mass and standard length (ANOVA, $F_{2,61} = 69.07$, n = 64, p < 0.001; $F_{2,63} = 36.71$, n = 66, p < 0.001, respectively). Body mass data were log-transformed for statistical analysis. Sexually immature seals were significantly lighter and shorter than both pregnant and non-pregnant animals (Table 3). Pregnant and non-pregnant seals showed no significant difference in body mass or standard length (Table 3).

length. Body mass was much more variable than length, likely explained by weight gain and loss associated with pregnancy. The sole 15-yr-old seal in the dataset showed an abnormally low body mass (48.6 kg) for its age. This particular seal was lactating at the time of capture and had given birth approximately 2 wk earlier. Such a low body mass is consistent with

Table 1. Parameter estimates (±SE, except where marked) of von Bertalanffy growth functions for standard length and body mass of harbor seals from the present study (L_∞ and M_∞ represent the asymptotic length and body mass respectively, a represents the rate of approach to the horizontal asymptote, and b represents the curvilinearity of that approach, see Eq. 1), compared with asymptotic standard length and body mass from previous studies. CL: confidence limits; GOA: Gulf of Alaska; BC: British Columbia

Study	Area	Standard length (cm)				Body mass (kg)			
		L_∞	n	a	b	W_∞	n	a	b
Present study	GOA	147.7 ± 2.6	65	0.32 ± 0.08	0.32 ± 0.05	82.2 ± 4.8	63	0.25 ± 0.08	0.83 ± 0.17
Pitcher & Calkins (1979)	GOA	144.8 ± 1.1[a]	134			76.5 ± 3.0[a]	93		
Bishop (1967)	GOA	155	141			68	140		
Bigg (1966)	BC	150	86			65	57		
[a]Calculated standard length (±95% CL), using adult seals ≥7 yr of age, and body mass (±95% CL) using adult seals ≥10 yr of age									

Ovary volume also differed significantly based on the reproductive status of the individual (ANOVA, $F_{3,101} = 115.5$, n = 105, p < 0.001). Ovary volume data were log-transformed for statistical analysis. Ovaries of immature animals had a significantly smaller volume compared with those of sexually mature animals (Table 3). The ovary on the active side of the repro-

Table 2. ANCOVA results and estimated implantation dates and growth rates for fetal measurements. ANCOVA results indicate no significant differences (α = 0.05) in growth for male and female harbor seal fetuses in the Gulf of Alaska for all measurements. The estimated implantation dates and growth rates were derived from the linear regression of each measurement against day of the year for male and female fetuses combined

| Measurement | ANCOVA | | | | Estimated implantation date | Growth rate (d^{-1}) |
| | Slopes | | Intercepts | | | |
	p	F	p	F		
Standard length	0.94	0.006	0.63	0.23	3 Oct	0.33 cm
Curvilinear length	0.32	1.0	0.50	0.57	17 Oct	0.50 cm
Fetal mass$^{1/3}$	0.28	1.2	0.90	0.015	25 Sept	0.09 $g^{1/3}$
Axillary girth	0.62	0.26	0.62	0.26	5 Oct	0.25 cm
Skull length	0.61	0.26	0.86	0.032	25 Sept	0.036 cm
Condylobasal length	0.86	0.032	0.36	0.87	25 Sept	0.069 cm
Skull width	0.61	0.27	0.84	0.043	28 Sept	0.043 cm
Zygomatic width	0.98	0.001	0.81	0.062	22 Sept	0.039 cm

Fig. 4. Harbor seal fetal body growth in (a) standard length (n = 27), (b) curvilinear length (n = 25), (c) fetal mass$^{1/3}$ (n = 27), and (d) axillary girth (n = 24). Day 1 and Day 366 represent 1 January in consecutive years. Gray shaded areas: 95% confidence limits

ductive tract had a significantly greater volume than the ovary on the inactive side (Table 3). There were no significant differences between the ovary volume of the ovary on the inactive side of the reproductive tract and the ovaries of non-pregnant animals (Table 3). Interestingly, there was also no significant difference between the ovary volume of non-pregnant animals and the ovary on the active side of the reproductive tract (p = 0.063) (Table 3).

The examination of the total number of corpora (corpora lutea and corpora albicantia) in relation to age, standard length, and body mass revealed thresholds at which harbor seals become mature (Fig. 6). Animals did not mature until a minimum age of 3 yr (n = 81), a standard length of 122 cm (n = 67) and a weight of 48 kg (n = 64). The average ASM was estimated at 4.2 ± 0.7 (95% CI) yr, although the sample size limited the strength of this calculation as not all of the age classes had the sample size (n = 25) recommended by DeMaster (1978) (Table 4). Forty of the 85 female seals were determined to be sexually mature. Of those sexually mature seals, 27 were pregnant at the time of collection, equating to an overall 67.5% pregnancy rate that varies by age (Fig. 7). With the exception of 5 yr olds (n = 2), pregnancy rates at all ages were lower compared with Bigg (1966). Differences were greatest for ages 3 and 4.
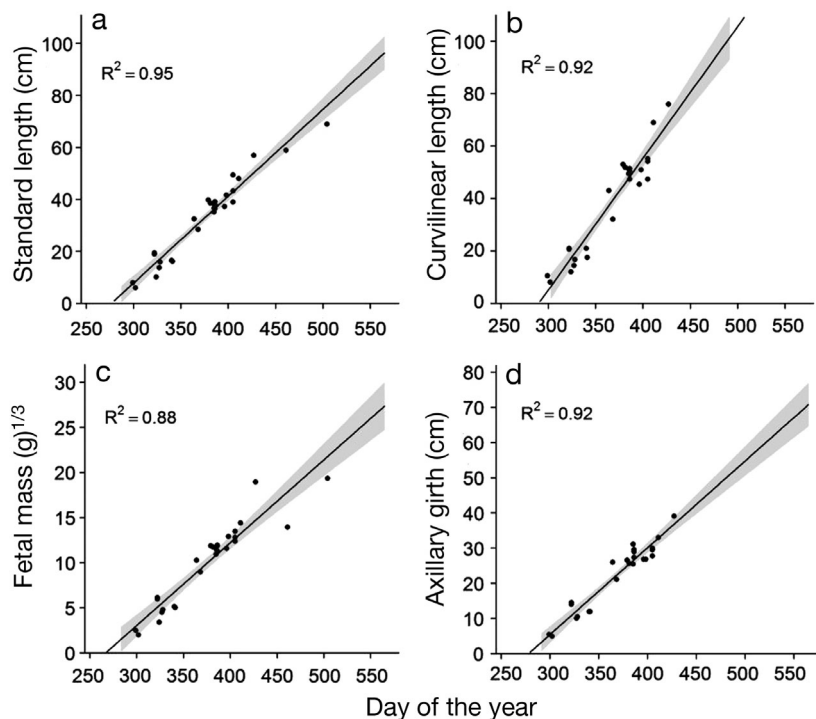
DISCUSSION

Postnatal growth

Standard length for harbor seals in the GOA suggests diminished growth since the 1960s (Table 1). Our asymptotic standard length is similar to the 150 cm found for harbor seals in British Columbia (Bigg 1966). However, our asymptotic body mass (82.2 ± 4.8 kg) is considerably heavier than that found for seals in British Columbia (65 kg) (Bigg 1966), and in the GOA previously (68 kg) (Bishop
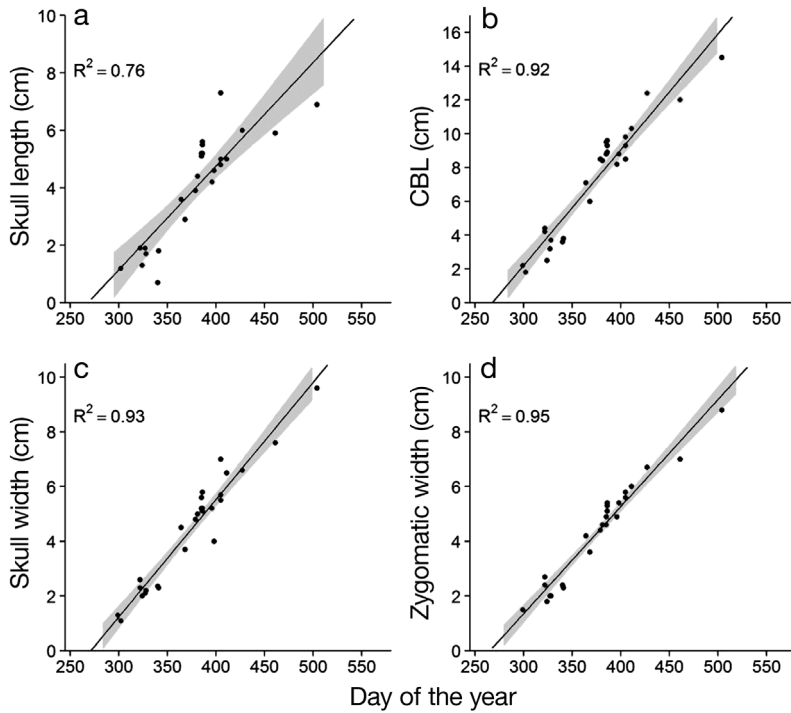
Fig. 5. Harbor seal fetal skull growth in (a) skull length (n = 26), (b) condylobasal length (CBL) (n = 27), (c) skull width (n = 27), and (d) zygomatic width (n = 26). Day 1 and Day 366 represent 1 January in consecutive years. Gray shaded areas: 95% confidence limits

higher asymptotic body mass may have been influenced by sampling time. Length is a more static measure as it is a reflection of skeletal growth, and therefore we see less variation among similarly aged animals, making it a more accurate measure of growth, provided measurements are taken consistently (Blundell & Pendleton 2008).

Fetal growth

The reproductive cycle of most pinnipeds is characterized by a period of embryonic diapause (Boyd 1991, Atkinson 1997). The timing and duration of this diapause varies between and within species (Bigg 1966, Bishop 1967, Bigg & Fisher 1974, Garlich-Miller & Stewart 1999, Chabot & Stenson 2000). Data in the present study indicate implantation for harbor seals in the GOA ranges from late September to early October. From the *x*-intercept of the linear least-squares regression of each fetal measurement, we estimated the implantation date for harbor seals in the GOA to be between 22 September and 17 October, with a mean (±SE) of 30 September ± 8 d. Implantation date for harbor seals has previously been estimated at early to mid-September near Tugidak Island in the 1960s (Bishop 1967) and early October for the GOA in the 1970s (Pitcher & Calkins 1979). Our estimate of 30 September aligns more closely with the latter (Pitcher & Calkins 1979) and indicates that the implantation date for harbor seals in the GOA may be later than that found for seals in the 1960s (Bishop

1967). The high asymptotic body mass found for our seals may be an indication of improved body condition. Body mass, however, showed considerably more variation than standard length. This is not surprising, as blubber levels, and consequently body mass, fluctuates greatly throughout the year due to reproduction, molting, and seasonality of prey (Härkönen & Heide-Jørgensen 1990). Our samples were collected throughout the year with the majority of the samples collected in November–March when seals have put on body fat and are in their fattest condition. Placental gestation also occurs at this time; therefore, a

Table 3. Mean values for body mass (kg), standard length (cm), and ovary volume (cm^3) by reproductive status. Non-pregnant animals were mature but not pregnant at the time of harvest. The 'pregnant-active' and 'pregnant-inactive' reproductive statuses represent the ovary on the pregnant and non-pregnant side of the reproductive tract, respectively. Data for body mass and ovary volume were log-transformed for statistical analysis, and means presented here are the back-transformed geometric means. Values not sharing a common letter are significantly different at p ≤ 0.05 by Tukey-Kramer multiple comparisons test

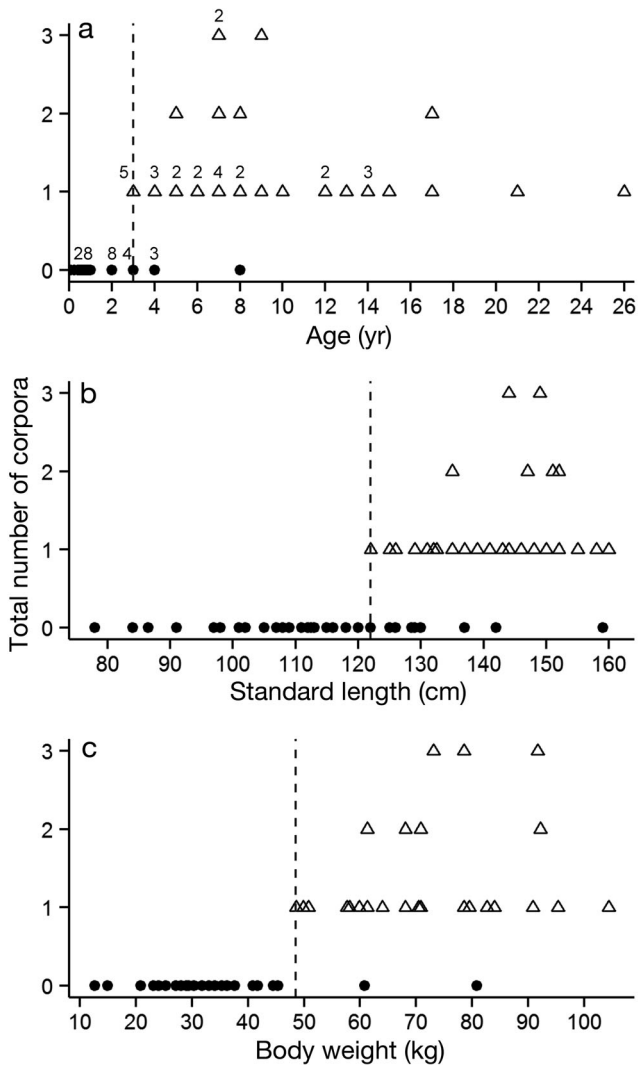| sReproductive status	Body mass (kg)			Standard length (cm)				Ovary volume (cm^3)		
	Mean	CI	n	Mean	CI	n		Mean	CI	n
Immature	31.9[a]	28.5, 35.7	35	111.9[a]	106.5, 117.3	36		1.2[a]	0.97, 1.4	45
Non-pregnant	65.4[b]	58.2, 73.6	8	143.5[b]	138.0, 149.0	8		6.4[b,c]	4.7, 8.8	10
Pregnant	75.7[b]	70.1, 81.7	21	140.6[b]	136.1, 145.1	22	Inactive:	6.0[b]	5.0, 7.1	25
							Active:	10.5[c]	9.3, 11.9	25

Fig. 6. Total number of corpora lutea and corpora albicantia in the right and left ovaries combined versus (a) age (n = 81), (b) standard length (n = 67), and (c) body mass (n = 64). The numbers above the symbols in (a) represent the sample size for each data point. ●: immature animals; △: mature animals; dashed line: threshold each animal crosses to become sexually mature

Table 4. Average age of sexual maturity (ASM) ± 95% CI, determined using the technique described by DeMaster (1978) for our data and previous studies in various locations

Location	Present study		Pitcher & Calkins (1979)		Bigg (1966)	
	ASM	n	ASM	n	ASM	n
Kodiak	4.5 ± 0.57	12				
Prince William Sound	3.3 ± 0.65	29	3.7 ± 0.3			
Southeast Alaska	6.5 ± 0.98	37				
Overall Gulf of Alaska	4.2 ± 0.74	82[a]	5.0 ± 0.43	183		
British Columbia					2.8 ± 0.35	138

[a]Overall sample size greater than the sum of the 3 regions due to additional samples from other regions in the Gulf of Alaska
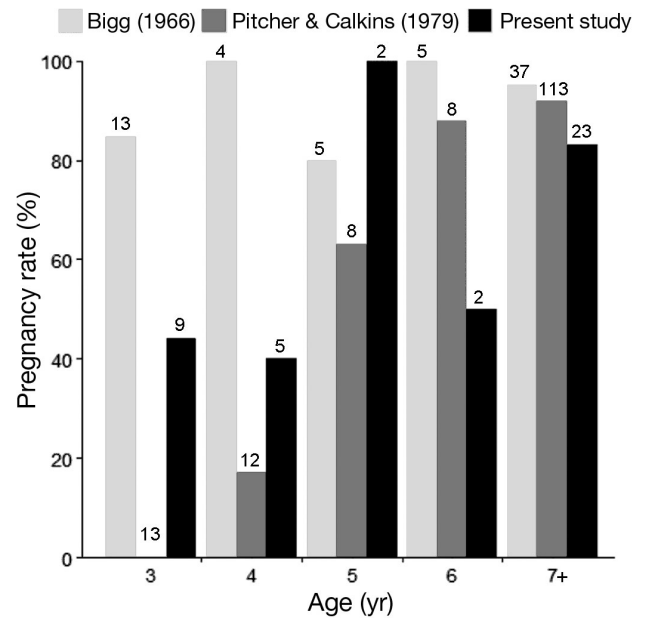

Fig. 7. Pregnancy rates by age for female harbor seals collected in the present study (1998–2006), by Pitcher & Calkins (1979), and by Bigg (1966). Numbers above the bars indicate sample size

1967). This later implantation date would likely result in a later mean pupping date if placental gestation has an obligatory duration. Seals at Tugidak Island and Aialik Bay were observed to give birth earlier in the mid-1960s and mid-1990s (early June) compared with the mid- to late 1970s (late June) (Jemison & Kelly 2001, Hoover-Miller et al. 2011). If an 8 mo active gestation period is assumed (Boyd 1991), a mean implantation date of 30 September would result in an early-June birthing peak for our study animals. Most newborn harbor seals in southcentral Alaska have been observed in the first half of June (Jemison & Kelly 2001, Hoover-Miller et al. 2011).

As we combined data for the entire GOA in our analyses, we cannot rule out the possibility of regional differences in fetal growth. Limited sample sizes did not allow us to examine the sub-regions separately, yet little variability in our data may indicate similar fetal growth rates and implantation date for harbor seals throughout the GOA. Also, the size of the blastocyst is not zero at the time of implantation, which may have resulted in a slight underestimation of implantation date and that implantation may be occurring later than calculated.

However, this effect is likely to be minimal considering that the size of the newly implanted blastocyst is extremely small (<0.1 g) (Pitcher & Calkins 1979).

The cause(s) of the termination of embryonic diapause and the subsequent initiation of implantation is not fully understood in pinnipeds. Some of the suggested controls include photoperiod (Temte 1994), and environmental conditions such as water temperature (Sergeant 1973) and maternal body condition (Boyd 1984, Stewart et al. 1989). In regards to implantation, Temte et al. (1991) and Temte (1994) found that harbor seals respond to a specific photoperiod, and consequently there is a latitudinal variation in the timing of pupping due to this response. However, populations north of 50°N latitude show no significant latitudinal effects like populations farther south, indicating populations such as those in the GOA are controlled by other factors than photoperiod (Temte et al. 1991). Boyd (1991) suggested that, for harbor seals in the North Pacific, food supply plays a significant role in the determination of implantation. In other pinnipeds, maternal condition affects the timing of implantation (Boyd 1984, Stewart et al. 1989). Implantation in northwest Atlantic harp seals *Phoca groenlandica* occurs after the seal attains a specific level of body fat (Stewart et al. 1989). Theoretically, implantation should occur when the conditions are right to supply the mother with the needed resources and energy to support a growing fetus and subsequently a suckling pup (Boyd 1984). Therefore, changes in implantation can provide insight into changes in environmental conditions. For example, an earlier than normal implantation date could indicate improved prey availability. Improved prey availability could lead to replenishment of fat levels in a reduced amount of time, shortening the length of embryonic diapause (Reijnders et al. 2010). Conversely, a later than normal implantation date, as found in our study, could indicate reduced or poorer prey availability. Reduced prey availability leads to poorer maternal body condition, which possibly results in prolonging the length of embryonic diapause and later birth (Reijnders et al. 2010).

In the present study, the rate of increase for fetal mass (0.09 $g^{1/3} d^{-1}$) was similar to that found for northwest Atlantic harp seals (0.10 $g^{1/3} d^{-1}$) (Stewart et al. 1989) and Atlantic walruses *Odobenus rosmarus rosmarus* (0.12 $g^{1/3} d^{-1}$) (Garlich-Miller & Stewart 1999). Taken together, these results indicate that fetal growth in mass is fairly consistent across different species of pinnipeds. Of the 8 fetal measurements used in this study, standard body length had the highest correlation coefficient and exhibited the least variance. Standard length is a reflection of skeletal growth, and therefore does not fluctuate as significantly as body mass and axillary girth.

Reproductive maturity

We identified thresholds that harbor seals in the present study exceeded to reach sexual maturity. These thresholds were 3 yr of age, 122 cm standard length, and 48 kg body mass. Using morphometric measurements to predict the actual age of harbor seals is confounded by substantial variability in length of immature seals and slow growth rates of adult seals. However, these threshold points can be useful for distinguishing immature from mature seals (Blundell & Pendleton 2008).

It is thought that pinnipeds, along with other mammals, must reach a certain critical mass before they can become sexually mature (Laws 1956, 1977, Boyd 1991). Moreover, it appears that body mass is a more definitive determinant of sexual maturity than standard length. With the exception of 2 seals in our dataset, all seals heavier than 48 kg were sexually mature. Thus, we estimated 48 kg to be the minimum size a harbor seal in the GOA must obtain before they can become sexually mature. Admittedly, this value is a rough estimate, which may show some regional differences within the GOA. Nonetheless, it may serve as a baseline against which to compare future changes over time and environmental conditions.

Age-specific reproductive rates were calculated for our data and compared with that of Pitcher & Calkins (1979). Our animals had higher reproductive rates at younger ages (3–5 yr), but lower reproductive rates at later ages (Fig. 7). Pitcher & Calkins (1979) calculated reproductive rates using only those animals collected between implantation and ovulation, and we only used post embryonic diapause pregnancies to ensure the data were comparable. Interestingly, the pregnancy rate data from Bigg (1966) were consistently higher than Pitcher & Calkins (1979), and only lower than the present study in one case that had a very small sample size (Fig. 7).

The average ASM for seals in the present study was estimated at 4.2 ± 0.7 yr (95% CI) and was slightly lower than that for harbor seals in the GOA in the 1970s (4.96 ± 0.43 yr) (Pitcher & Calkins 1979), but greater than that calculated for seals in British Columbia in the 1960s (2.8 ± 0.35 yr) (Bigg 1966) (Table 4). We calculated the average ASM for Bigg's (1966) data using the ovulation data presented in their paper and the technique described by DeMaster (1978).

When evaluated by region, our data revealed differences in average ASM, with southeast Alaska having a higher ASM compared with the Kodiak and Prince William Sound regions. However, the sample sizes for each region were too small to say definitively whether observed differences were significant. A later ASM for southeast Alaska may indicate that the population is being influenced by density-dependent effects, and may be at or near carrying capacity, as supported by the recent declines in Glacier Bay (Womble et al. 2010). The Kodiak and Prince William Sound regions may still be recovering from previous declines in population size, and may not be limited by density-dependent effects or resource limitation. Additional samples are needed to investigate this further.

Sampling biases and limitations

The data used in this study come from harvested animals and therefore do not represent a truly random sample. There is the possible bias of hunter selection and the availability of the seals to be harvested. For example, older age classes of adult seals were poorly represented in our data. However, important life history events for seals such as reproductive maturity and the majority of growth, typically occur within the first 5 yr of life, minimizing the effect of this bias on our data analyses.

CONCLUSION

Harbor seal reproduction is responsive to ecological change and can provide insights into top-down and bottom-up effects on population growth. Reproductive parameters measured by Bigg (1969b) for seals in British Columbia appear to represent maximal population growth (Allen & Angliss 2013) at a time after being culled to low levels, then released from that mortality (top down) pressure in an environment with apparently abundant food resources. In contrast, seals in the Gulf of Alaska, similarly released from bounty harvests, experienced a precipitous population crash (Pitcher 1990). High mortality associated with bounty harvests in the 1950s and 1960s may have artificially heightened reproductive rates (in response to top-down effects) relative to environmental conditions. Abrupt removal of that harvest pressure, due to implementation of the MMPA in 1972, in conjunction with bottom-up effects of the regime shift of the mid-1970s, may have exac-

erbated an imbalance of top-down and bottom-up effects with pronounced, adverse population-level consequences. Bishop's (1967) research was conducted prior to major declines of harbor seal populations in Alaska, and may represent near carrying capacity abundance at locations experiencing heavy harvests. As seen in British Columbia, with lower seal density (resulting from harvests) and a predicted increase of per-capita prey resources, it would be expected that growth would be faster and sexual maturity achieved earlier (Stearns 1992). Our data suggests that bottom-up constraints may have relaxed since the 1970s, allowing reproduction at an earlier age than during the 1970s, but reproduction and body growth may still be constrained as one would expect with populations tracking resources. Unexpectedly, however, delayed reproduction, comparable to that detected in the Aleutian Islands, prior to population decline in that region (Burns & Gol'tsev 1984, Small et al. 2008) was particularly evident in our samples from southeast Alaska (Table 4), indicating a potential for widespread population declines like those observed in Glacier Bay (Womble et al. 2010).

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