Growth and reproduction of Atlantic walruses (Odobenus rosmarus rosmarus) in Foxe Basin, Northwest Territories, Canada

> by Joel Garlich-Miller

> > A thesis

presented to the University of Manitoba in fulfillment of the

thesis requirements for the degree of

Masters of Science

in

Department of Zoology

Winnipeg, Manitoba

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GROWTH AND REPRODUCTION OF ATLANTIC WALRUSES (<u>Odobenus rosmarus rosmarus</u>) IN FOXE BASIN, NORTHWEST TERRITORIES, CANADA

BY

JOEL GARLICH-MILLER

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements for the degree of

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MASTER OF SCIENCE

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This thesis is dedicated to Francis "Bud" Fay, whose pioneer walrus studies laid the foundations for this and many other research projects. His unexpected passing on June 9th, 1994 was a great loss to the research community.

Abstract

The growth and reproductive biology of Atlantic walruses (Odobenus rosmarus rosmarus) were investigated using morphological data, reproductive organs, and ageing structures collected from walruses harvested by Inuit subsistence hunters in 1988, 1991-1993 from Foxe Basin, NT, Growth curve parameters were used to describe Canada. somatic growth and to investigate sexual size dimorphism. Male walruses reached a larger final body size than did females. Males reached an asymptotic size of 315 cm in standard length (n = 103) and 849 kg in mass (n = 14). Females attained an asymptotic standard length of 276 cm (n = 90) and an asymptotic mass of 633 kg (n = 11). The predictive equation relating mass (M, kg) to standard length (SL, cm) for both sexes combined was: $M = 1.82 \times 10^{-4} (SL^{2.68})$ (n = 25). Comparing growth parameters with values reported for other collections of temporally and geographically isolated populations of walruses indicated that: i) the growth pattern of male Foxe Basin walruses was the same in the 1990's as in the 1950's; ii) for both sexes, Foxe Basin walruses were significantly larger than walruses sampled from northern Hudson Bay in the 1950's; and iii) female Atlantic walruses sampled from Foxe Basin were larger than female Pacific walruses (Odobenus rosmarus divergens) collected in Alaska during the 1970's.

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The reproductive status of sampled walruses was investigated by macroscopic examination of the reproductive organs. For males, no criteria were found for distinguishing between sexually mature and immature testes. For females, no evidence of past or present ovulation was found in specimens less than 5 years old. The poor representation of juvenile and adolescent animals precluded firm conclusions on the average age of sexual and breeding maturity. The ovulation frequency of 64 mature females (0.52) indicated biennial ovulation, while the pregnancy rate (0.33) and birth rate (0.30) suggested that females gave birth once every three years. Anomalies and pathologies of the uterus were observed in 3 females. The sex ratio of 17 fetuses was not significantly different from 1:1. Fetuses increased 2.9 mm $* d^{-1}$ in crown-rump length and 0.12 $g^{1/3} * d^{-1}$ in mass over the range of collection dates. Based on the inverse regressions of fetal growth, implantation occurs approximately June 30th.

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Acknowledgements

I would like to take this opportunity to thank my supervisor, Dr. R.E.A. Stewart, for introducing me to the fascinating world of arctic marine mammal research. Through the course of this study, Dr. Stewart provided me with strong support and insightful guidance as well as giving me considerable freedom to make and act on my own decisions. The opportunity to face the challenges of this research project resulted in tremendous personal growth, for which I am deeply grateful.

This research would not have been possible without the help and cooperation of many people from the communities of Hall Beach and Igloolik. I would like to thank all of the walrus hunters who contributed biological samples to the project. In particular I would like to thank Apayata Kortiek, Zacharias Kunuk and Solomon Quanatsiaq for their hospitality and companionship during field seasons. Jake Irqirpiriaq (Government Liaison Officer, Hall Beach) and Brad Parker (Renewable Resources Officer, Igloolik) provided invaluable logistical support during field operations.

The theoretical component of this research was enriched by conversations on life-history theory with Barbara Stewart. The thesis was also improved by the constructive

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comments of Dr. R.A. MacArthur and Dr. K.W. Stewart of the Department of Zoology, University of Manitoba, and by Stuart Innes of the Freshwater Institute, Department of Fisheries and Oceans.

The research was funded by the Department of Fisheries and Oceans. Additional support was received in the form of a University of Manitoba Graduate Fellowship. Field support was provided by the Eastern Arctic Scientific Research Laboratory.

Finally, I would like to recognize my wonderful wife Sharon Desbarats, who put up with my long field seasons and late hours, and who helped me maintain a balanced perspective of all things important in life.

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General Introduction

The walrus (Odobenus rosmarus), one of the worlds' largest pinnipeds, is the only extant species of the family Odobenidae. Two subspecies of walrus are generally recognized; the Pacific walrus (O. r. divergens Illiger 1811) is found primarily in the Bering and Chuckchi seas, while the Atlantic walrus (O. r. rosmarus Linnaeus 1785) is distributed throughout the north Atlantic and Arctic oceans (Reeves 1978; Fay 1982; Richard and Campbell 1988).

Most assumptions on walrus life history are based upon data collected from Pacific walruses. At birth, Pacific walrus calves are approximately 65 kg in mass and 113 cm in standard length. After the first few years of life, the growth patterns of males and females diverge. The female growth rate declines rapidly until a maximum body size is reached at approximately 10 years of age. Adult females attain a mean body mass of 830 kg and standard length of 270 cm. Males do not achieve full physical maturity until at least 15-16 years of age. Adult males attain a mean body mass of 1200 kg and mean standard length of 320 cm (Fay 1982).

Male Pacific walruses attain sexual maturity at 7-10 years of age but are unlikely to gain access to mates until they reach full somatic maturity (Fay 1982). Females normally attain sexual maturity at 5-7 years of age and give birth to a single calf at 2-3 year intervals (Fay 1982). Estrus and mating normally occur in February-March (Fay et al. 1984; Kibal'chich 1988). Pregnancy is characterized by a period of embryonic diapause during which the embryo remains unattached in the uterine cornua for 3-4 months (Fay 1982; Fay et al. 1984). Implantation of the blastocyst occurs mainly in June, after which the fetus undergoes approximately 11 months of active gestation (Fay 1982; Fay et al. 1984). Parturition usually occurs in late May (Fay 1982; Fay et al. 1984; Kibal'chich 1988).

Quantitative information on the life history characteristics of the Atlantic walrus is limited. The objective of this study was to quantify aspects of growth and reproduction in the Atlantic walrus and to interpret these data in terms of life history evolution. The thesis is presented in two parts which examine growth and reproduction, respectively. The results of the two sections are discussed in the context of life history tactics and population dynamics.

Growth and sexual dimorphism of Atlantic walruses (Odobenus rosmarus rosmarus) in Foxe Basin, Northwest Territories, Canada

Part I

Introduction

In pinnipeds, growth is generally characterized by: *i*) an initial phase of rapidly increasing body size, *ii*) a gradual deceleration of somatic growth, and *iii*) a final maximum body size (Laws 1956, 1959; McLaren 1993). Sexual dimorphism in size is common among polygynous species (e.g. Laws 1956; McLaren 1993) and is a characteristic of the Atlantic walrus Odobenus rosmarus rosmarus (Mansfield 1958). Among dimorphic species, the growth pattern of males often includes a period of accelerated growth at puberty (Laws 1956; McLaren 1993) and such a pattern has been reported for male Pacific walruses (Odobenus rosmarus divergens) (Fay 1982).

There are few published growth data for Atlantic walruses. Mansfield (1958) presented length-at-age data for 83 male and 39 female walruses collected from Foxe Basin and northern Hudson Bay in the early 1950's. More recently, Knutsen and Born (1991) obtained length and mass measurements from 19 Atlantic walruses collected in Northwest Greenland.

Growth curve parameters provide a tool for examining sex-linked and inter-specific differences in body size (e.g. McLaren 1993), and provide an index by which temporal

changes within a population can be measured (e.g. Sergeant 1973; Innes *et al.* 1981). McLaren (1993), fitted non-linear growth curves to length-at-age data for Atlantic walruses from Foxe Basin and Hudson Bay (Mansfield 1958) and Pacific walruses from Alaska (Fay 1982). He reported that the male Foxe Basin walruses reached a larger asymptotic length than did animals sampled from either Hudson Bay or Alaska.

In the present study, four growth models were evaluated and the growth parameters of the best model were used to quantify growth and test for sexual dimorphism in Atlantic walruses from Foxe Basin. The relationship between body mass and various linear measurements was also examined. Finally, growth parameters were compared to values published by McLaren (1993) for collections of temporally and geographically isolated populations of walruses.

Materials and Methods

Sampling

Walruses were sampled intermittently over a 10 year period (1983-1993) as part of ongoing Department of Fisheries and Oceans (DFO) studies. Samples were collected in connection with normal subsistence hunting activities of the communities of Hall Beach and Igloolik, Northwest Territories (NT), Canada (Fig. 1.1). The animals taken by the two communities were assumed to come from a common population inhabiting northern Foxe Basin (Richard and Campbell 1988). Between-year variations in measured variables over the range of collection years were assumed to be minimal and data for all years were pooled. Due to a narrow range of sampling dates across collection years (July 6 to August 9), seasonal differences were not examined.

Morphological measurements were made in accordance with the guidelines of the American Society of Mammalogists (1967). For all sampling years, standard length (cm) and axillary girth (cm) were measured to the nearest centimetre with a steel measuring tape. In 1992-93, girth measurements at eyes, navel and pelvis, and body mass (kg) were added to the sampling protocol. Mass was determined for 25 whole animals positioned on a rigid aluminum and nylon stretcher

Figure 1.1. Foxe Basin study area.



(Knutsen and Born 1991) resting on three load cells (Strainsert, model FL 2.5 U(C)-2S6KT) (Fig. 1.2). A digital transducer readout (Acrotech, model IRC-404A), connected to the load cells displayed mass with a theoretical precision of 1 kg. No allowances were made for blood loss.

Ages were estimated by counting annual incremental layers (growth layer groups) in the cementum of a lower canine tooth (Garlich-Miller et al. 1993). Ages were estimated in whole years, representing the age at last birthday. In young pinnipeds, size can change considerably over the course of a year and fitting growth curves to nominal ages can produce misleading results (McLaren 1993). Following McLaren (1993), ages were adjusted to a fraction of a year. Based on a birth period of mid-late May (Mansfield 1958) and a mean collection date of July 24th, 2 months (0.16 years) were added to all sample ages. This adjustment did not significantly alter growth curve parameters (t-test, P > 0.05) and produced better size predictions for young of the year. Using adjusted ages also standardized the results with McLaren (1993), permitting cross-study comparisons.

Figure 1.2. Measurement of body mass of a 720 kg adult male Atlantic walrus (*Odobenus rosmarus rosmarus*). One of the load cells positioned under the stretcher (arrow) can be seen to the right.



Growth models

Various non-linear growth equations have been used to describe growth in pinnipeds (e.g. Laws 1959; Innes et al. 1981; McLaren 1993; Rosas et al. 1993). The following four growth models were evaluated for Atlantic walruses sampled from Foxe Basin, NT, Canada:

1) the Richards equation (Richards 1959)

$$S_{t} = A (1 - e^{-k(t - t_{o})})^{m}$$

2) the Gompertz equation (McLaren 1993)

$$S_{+}=A(e^{(-e^{-kt+kt_{o}})})$$

3) the von Bertalanffy equation (von Bertalanffy 1957)

 $S_{t} = A (1 - e^{-k(t - t_{o})})$

4) a constrained Richards equation (McLaren 1993)

$$S_{t} = A (1 - e^{-k(t - (-0.87))})^{m}$$

where S_t is body size (length or mass) at age = t, A is asymptotic size, k, t_o and m are fitted constants and e is the base of natural logarithms (~ 2.71828183).

Equations 2-4 are special cases of the general Richards function (Eq. 1) which was originally used to describe indeterminate growth in plants (Richards 1959). The Gompertz model has been used to describe growth in

beluga whales (Delphinapterus leucas) (Stewart 1994), harp seals (Phoca groenlandica) (Innes et al. 1981) and other pinniped species (McLaren 1993). The von Bertalanffy equation has been widely used to describe asymptotic growth in fish (Misra 1986), but has also been applied to a variety of long-lived vertebrates such as elephants (Loxodonta africana africana)(Laws et al. 1975), polar bears (Ursus maritimus) (Kingsley 1979), sea lions (Otaria flavescens) (Rosas et al. 1993) and harp seals (Innes et al. 1981). McLaren (1993), fitted a constrained Richards equation to growth data for a number of pinniped species. This equation differs from the 4 parameter Richards function in that ${\tt t_o}$ is set a priori as an age scale correction. Following McLaren (1993), the constant t_o was set at -0.87 (years) based on the estimated period of active gestation for Pacific walrus fetuses (Fay 1982).

Non-linear, least-squares regression procedures (SAS Institute Inc. 1985) were used to fit the growth equations to age-related length and mass data. Data for each sex were examined independently to test for sexual dimorphism (Mansfield 1958). The four growth models were evaluated by comparing their respective R^2 values (Misra 1986; Stewart 1994) and asymptotic size estimates were compared using *t*tests (Glantz 1992).

Sexual dimorphism

To test for sexual dimorphism, male and female growth curve asymptotes were compared using a *t*-test for unequal sample sizes and unequal variances (Glantz 1992). Sexrelated differences in growth rates were described by plotting the differences in predicted length (*PL*) between male and female growth models ($PL_{MALE} - PL_{FEMALE}$) as a function of age. The slope of the least-squares regression equation relating differences in *PL* with age in sub-asymptotic animals was used to quantify differences in growth rates.

A characteristic of asymptotic growth equations is that asymptotic size continues to increase as t (age) approaches infinity (Wiig 1985). For each sex the age at which 95 % of asymptotic length was achieved was calculated and used as an indicator of the length of the growth period, and as an index for comparing the growth periods of males and females.

To test for the occurrence of a secondary growth spurt in male walruses, automated curve-fitting software was applied to length-at-age data (TableCurveTM 1992). A total of 2560 different models (including linear, quadratic and polynomial models) was assessed for significant increases in R^2 over the best monotonic growth model.

Mass-Length relationships

The relationships between mass (kg) and various linear measurements (cm) were examined using \log_{10} transformed data. Mass was examined as a function of standard length and girth measurements at eyes, axilla, umbilicus and pelvis using a stepwise regression technique in SAS, where variables with a partial P \leq 0.01 were included in the equation (SAS Institute Inc. 1985, MAXR procedure). Predictive equations for males and females were tested for equality with a test of coincidence using SigmaStatTM (Bagdasian *et al.* 1992).

Comparisons with other studies

Comparisons between growth curve asymptotes from this study and those presented by McLaren (1993) for Atlantic and Pacific walruses were made using t-tests for unequal sample sizes and unequal variances (Glantz 1992). For comparative purposes, the analysis was restricted to constrained Richards functions applied to measurements of standard length (McLaren 1993). Where significant differences in asymptotic length were found, the slope of the linear leastsquares regression equation relating differences in PL with age in sub-asymptotic animals was used to quantify differences in growth rates. The ages corresponding with 0.95(asymptote) of the two models were used to compare growth periods. Mass-length equations for walruses sampled from Foxe Basin and from Greenland (Knutsen and Born 1991) were tested for equality with a test of coincidence using SigmaStat[™] (Bagdasian *et al.* 1992). Two decapitated walruses sampled by Knutsen and Born (1991) (ID No. 6 and 7) were not included in this analysis.

Results

Sampling

Morphological and age data from 103 male and 90 female walruses were examined. Differences in sample sizes for some analyses were the result of incomplete data.

Growth models

For each sex, the four growth models produced similar \mathbb{R}^2 values when applied to measurements of standard length (Table 1.1) and estimates of asymptotic length were not significantly different between models (P > 0.05). When fitted to mass measurements for male walruses, the von Bertalanffy and constrained Richards equations produced similar R^2 values and asymptotic mass estimates (P > 0.05), while convergence criteria were not met for Richards and Gompertz models (Table 1.1). When applied to mass measurements for female walruses, the four growth models produced similar R^2 values and the asymptotic size estimates of the models were not significantly different (P > 0.05). Because the constrained Richards model (Table 1.1; Figs. 1.3 and 1.4) converged for all data sets, predicted 85-89 % of the variance in all instances and facilitated comparison with the only other fitted growth curves for walruses (i.e. McLaren 1993), it was selected to describe somatic growth for the remainder of this paper.

Table 1.1 Parameter estimates (\pm 1SE) of four growth models fitted to morphometric data from Atlantic walruses (Odobenus rosmarus rosmarus) from Foxe Basin, NT.

Equations	sex	А			k		t _o	m	n	R ²
Standard lengt (1)Richards	h (cm M F) 315.1 <u>+</u> 278.4 <u>+</u>	3.8	0.13 0.16	+ + +	0.04	-5.10 ± 0.47 -0.08 ± 0.27	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	103 90	0.88
(2)Gompertz	M F	309.0 <u>+</u> 273.6 <u>+</u>	2.3	0.25 0.38	+ + +	0.01 0.04	-0.65 ± 0.14 -0.54 ± 0.11	-	103 90	0.87 0.86
(3)von Bertalanffy	M F	311.6 <u>+</u> 275.1 <u>+</u>	2.8	0.19 0.31	+ + -	0.02	-2.71 ± 0.36 -1.86 ± 0.30	- -	103 90	0.87
(4)constrained Richards	M F	315.2 <u>+</u> 276.6 <u>+</u>	3.8 3.4	0.15 0.25	<u>+</u> +	0.02	-0.87* -0.87*		103 90	0.88 0.86
Mass (kg)										
(1)Richards	M F	648.5 <u>+</u>	124.7	0.18	-d. ±	id not 0.28	converge- -0.07 <u>+</u> 0.84	0.68 <u>+</u> 0.87	14 11	0.89
(2)Gompertz	M F	620.5 <u>+</u>	39.9	0.36	-d: ±	id not 0.10	converge- 1.76 <u>+</u> 0.38	-	14 11	0.89
(3)von Bertalanffy	M F	857.6 <u>+</u> 634.8 <u>+</u>	66.0 62.4	0.21 0.24	+ +	0.10 0.14	-0.15 ± 0.63 -0.42 ± 0.60		14 11	0.85 0.89
(4)constrained Richards	M F	849.3 <u>+</u> 633.4 <u>+</u>	60.1 66.4	0.25 0.26	+ + +	0.14 0.19	-0.87* -0.87*	-	14 11	0.85 0.89

* Constrained a priori (McLaren 1993).

Figure 1.3. Standard length (L) of 103 male (A) and 90 female (B) Atlantic walruses (*Odobenus rosmarus rosmarus*) in relation to age (t). Curves were fitted according to a constrained Richards growth model, where $t_0 = -0.87$.





Figure. 1.4. Body mass (M) of 14 male (A) and 11 female (B) Atlantic walruses (*Odobenus rosmarus rosmarus*) in relation to age (t). Curves were fitted according to a constrained Richards growth model, where $t_0 = -0.87$.




Age (years)

Sexual dimorphism

Sexual dimorphism in standard length was not evident in young of the year (males: $\bar{x} = 127.25$ cm, sd = 6.95, n = 4; females: $\bar{x} = 123.57$ cm, sd = 3.41, n = 7: t = 1.20, df = 9, P > 0.05). Although the number of mass measurements for young of the year were insufficient for statistical analysis, the range (70-78 kg) in mass for two females and one male was small.

Sexual size dimorphism was apparent in adult animals (Figs. 1.3 and 1.4). Males were were significantly larger than females in both asymptotic length (males: A = 315.2 cm, SE = 3.8, n = 103; females: A = 276.6 cm, SE = 3.4, n = 90: t = 7.21, df = 191, P < 0.05) and asymptotic mass (males: A = 849.3 kg, SE = 60.1, n = 14; females: A = 633.4 kg, SE =66.4, n = 11 : t = 2.35, df = 23, P < 0.05).

Differences in predicted length (*PL*) between male and female growth models ($PL_{MALE} - PL_{FEMALE}$) increased with age (Fig. 1.5). The least-squares regression relating differences in *PL* with age in sub-asymptotic animals had a significant, positive slope (slope = 1.47 cm/year, *SE* = 0.26, t = 5.5, df = 9, P < 0.05), indicating that males have a higher growth rate than females. Males also grew for a longer period than females. The female growth model

Figure 1.5. Differences in predicted length (*PL*) of male and female Atlantic walruses (*Odobenus rosmarus rosmarus*) in relation to age. The curve represents agespecific differences between male and female growth models. Vertical reference lines indicate the predicted age at which (A) females and (B) males attain 95% of asymptotic length.



predicted that 95 % of asymptotic length was achieved by 9 years of age, while the model for males did not achieve 95 % of the asymptote until 14 years of age.

A secondary acceleration in somatic growth was not apparent in the length-at-age data of sampled male walruses (Fig. 1.3A). Fitting continuous functions to growth data did not improve the fit over monotonic growth models (P >0.05).

Mass-Length relationships

The logarithm of standard length (cm) was the best explanatory variable for predicting body mass for both male and female walruses. The addition of girth measurements did not significantly (P > 0.5) improve the regression equations.

Mass-length relationships were not significantly different between sexes ($F_{1,21} = 1.08$, P > 0.05). Data for males and females were pooled (Fig. 1.6) and the resulting equation relating mass (kg) to standard length (cm) was:

Mass =
$$1.82 \times 10^{-4}$$
 (SL^{2.68}) ($R^2 = 0.98$, $F_{1,23} = 1000$).

The exponent 2.68 was significantly different (t = 3.85, df = 23, P < 0.05) from 3.00. This equation produced

Figure 1.6. Log₁₀-mass as a function of log₁₀-length for 14 male and 11 female Atlantic walruses (*Odobenus rosmarus rosmarus*). Open circles represent females, solid circles represent males. Line was fit according to leastsquares linear regression.



significantly lower ($F_{1,38} = 9.53$, P < 0.05) estimates of mass than did the isomorphic equation generated for 17 Atlantic walrus harvested in Greenland (Knutsen and Born 1991):

Mass = 6.79 *
$$10^{-5}$$
 (SL^{2.88}) ($R^2 = 0.98$ $F_{1.17} = 699.6$).

Comparisons with other studies

No significant difference in asymptotic length was observed between males sampled in this study and those sampled from the same region circa 1950 (Table 1.2; t = 0.02, df = 191, P > 0.05). Data for Foxe Basin females collected in the 1950's were insufficient for analysis (McLaren 1993).

The asymptotic lengths of Foxe Basin walruses sampled for this study were significantly larger than those reported for Hudson Bay walruses sampled circa 1950 (Table 1.2; males: t = 2.87, df = 141, P < 0.05; females: t = 2.85, df =117, P < 0.05). Age-specific differences in growth models ($PL_{FOXE \ BASIN} - PL_{HUDSON \ BAY}$) produced positive slopes in subasymptotic age classes (males_(0-12 years): slope = 2.16 cm/year, SE = 0.13, t = 6.2, df = 11, P < 0.05; females_(0-8 years): (slope = 3.00 cm/year, SE = 0.28, t = 6.8, df = 7, P <0.05), indicating that Foxe Basin animals had higher growth rates than animals from Hudson Bay (Fig. 1.7).

Sub-species			
Locality	sex	n	A
			······································
0.r. rosmarus			
Foxe Basin	М	103	315.2 ± 3.8
(this study)	F	90	276.6 ± 3.4
Foxe Basin [*]	М	31	316.3 ± 6.9
(McLaren 1993)	F	Not available	
Hudson Bay [*]	М	40	292.8 ± 7.7
(McLaren 1993)	F	29	258.6 ± 3.6
0. r. divergens			
Alaska**	М	168	310.1 ± 6.9
(McLaren 1993)	F	92	259.8 ± 4.1

TABLE 1.2. Asymptotic lengths (A (cm) \pm 1 SE) of walruses (Odobenus rosmarus) from various populations and periods.

* Data originally presented by Mansfield (1958).

** Data originally presented by Fay (1982).

Figure 1.7. Differences in predicted length (*PL*) of Atlantic walruses (*Odobenus rosmarus rosmarus*) from Foxe Basin and Hudson Bay. The curves represent age-specific differences between (A) male and (B) female growth models for Foxe Basin (this study) and Hudson Bay (McLaren 1993) walruses ($PL_{FOXE BASIN} - PL_{HUDSON BAY}$). Vertical reference lines indicate the predicted ages at which Hudson Bay walruses attain 95% of asymptotic length.





For Foxe Basin growth models, 95 % of predicted asymptotic length was attained by the age of 9 years in females and 14 years in males. The corresponding ages for Hudson Bay walruses were 8 and 12 years for females and males respectively.

Although there was not a significant difference in asymptotic length between Foxe Basin and Alaskan males (Table 1.2; t = 0.55, df = 269, P > 0.05), Foxe Basin females were significantly longer than their Alaskan counterparts (Table 1.2; t = 3.13, df = 180, P < 0.05). Age-specific differences in female growth models ($PL_{FOXE BASIN} - PL_{ALASKA}$) produced positive slopes in subasymptotic age classes (0-9 years): (slope = 1.29 cm/year, SE = 0.29, t = 6.8, df = 8, P < 0.05), indicating that Foxe Basin females had higher growth rates than their Pacific walrus counterparts from Alaska. The growth periods of Foxe Basin and Alaskan females were similar with 95% of asymptotic length being achieved by the ages of 9 and 10 years respectively.

Figure 1.8. Differences in predicted length (*PL*) of female Atlantic walruses (*Odobenus rosmarus rosmarus*) from Foxe Basin and female Pacific walruses (*Odobenus rosmarus divergens*) from Alaska. The curve represents the agespecific differences between growth models ($PL_{\rm FOXE\ BASIN}$ - $PL_{\rm ALASKA}$). The vertical reference line indicates the predicted age at which Alaskan females attain 95% of their asymptotic length.



Discussion

Sampling errors and biases

Somatic growth generally refers to changes in body size of an individual over time. In this study, sampling for growth was restricted to morphological data collected from a cross-section of the Foxe Basin walrus population. Growth curves derived from cross-sectional data characterize the mean size of individuals surviving to successive age classes and are subject to sampling biases. Hunter selection bias and size-dependent mortality introduce error into estimates of growth rates and adult body size (McLaren 1993). Although random sampling and selective harvest data are diametric, Leberg et al. (1989) found that growth curve asymptotes were relatively robust to various simulated biases associated with harvest data. Furthermore, for the purpose of cross-study comparisons, it is not unreasonable to assume that selection biases present in these data are similar to those associated with other harvest studies of walruses (eg. Mansfield 1958; Fay 1982; Knutsen and Born 1991).

Fitting growth curves to cross-sectional data also assumes that age-specific growth rates are constant over time. The link between population density, resource availability and juvenile growth rates has been established

for other pinniped species (Laws 1956; Sergeant 1973; Innes et al. 1981). Changes in population density or resource availability could result in different growth rates for past and present cohorts. Unfortunately, harvest and census statistics are insufficient to determine whether the population density of Foxe Basin walruses has changed significantly over the past 30 years.

An accurate method of age determination for sampled animals is a prerequisite to fitting growth curves to crosssectional data. Leberg et al. (1989) found that assigning individuals to incorrect age classes biased asymptotic size and increased the variance of all parameter estimates. Counts of incremental cemental growth layer groups (GLG's) has been the standard method of estimating age in walruses (Mansfield 1958; Fay 1982; Garlich-Miller et al. 1993). Fay (1982) examined the teeth of 18 captive-reared walruses ranging from 0 to 15 years of age and found that the number of cemental layers closely corresponded to the known age of the animal in years. Errors associated with age estimation in walruses generally increase with age. Garlich-Miller et al. (1993), found minimal between-reader differences in walrus teeth with less than 10 cemental GLG's, while age estimates in older age classes occasionally exceeded a 10 % coefficient of variation among readers. However, errors associated with age estimation in physically mature animals

(after somatic growth is complete) are unlikely to affect the dynamics of the growth models.

The precision of age estimates for walruses is presently restricted to whole years (Garlich-Miller *et al.* 1993). Leberg *et al.* (1989) found that the precision of age estimates had little effect on growth parameters fitted to a simulated growth model for white tail deer (*Odocoileus virginianus*). Although walrus calves aged "0" years were estimated to have been born 2 months prior to collection, (and adjusted accordingly) the length of the birth period is not known precisely. Because of the rapid postnatal growth of neonates (Laws 1959) and the variability of collection dates, predictions of size at birth must be interpreted cautiously.

Growth models

When convergence criteria were met, no one age-related growth function was superior to any other for length or mass data. A constrained Richards function, permitted comparisons with McLarens' (1993) comprehensive analyses. In this equation (referred to by McLaren as a "generalized" von Bertalanffy model) t_0 was set a priori as an age-scale correction, representing the time between the initiation of embryonic growth and birth. Fitting t_0 as a constant implies that embryonic growth follows the manner described

by the equation for postnatal growth. McLaren (1993) acknowledges that prenatal growth (in body-length) is essentially linear and is not well described by non-linear functions. However, setting t_o as a constant served to anchor the lower end of the growth curves where data for younger animals were under-represented (McLaren 1993).

For his multi-species analysis of growth in pinnipeds, McLaren (1993) excluded all data from young of the year on the supposition that young pinnipeds achieve most of their first year growth during a short intense nursing period. While this may hold true for some phocid species (particularly in mass; see Stewart and Lavigne 1984), this constraint is unjustified for walruses. Walrus calves nurse for up to two years (Mansfield 1958; Fay 1982; Miller and Boness 1983; Fisher 1989) and have a low rate of postnatal growth relative to phocid pups (Fay 1982). The inclusion of calves < 1 year of age in the present analysis did not significantly alter growth curve parameters or affect the results of cross-study comparisons.

The shape of the plotted differences in predicted length from walruses sampled from various locations varied from one comparison to another. Most of the irregularity occurred in predicted differences at younger age classes. It should be re-emphasized that these comparisons are based

on predicted models and are therefore subject to biases associated with modelling.

Leberg et al. (1989) found that a non-uniform sampling distribution could affect the shape of a growth curve and result in unrealistic size estimates for younger age classes. Young animals were under-represented in all models compared. By excluding data from animals < 1 year of age, McLaren (1993) biased the shape of his growth curves towards older age classes. This is apparent in his models for Hudson Bay walruses, where the predicted size of calves < 1 year of age are substantially larger than indicated by the raw data.

Sexual dimorphism

Sexual dimorphism in mean size was not apparent in newborn walrus calves, consistent with other studies of full-term fetuses (Fay 1982) and newborn calves (Mansfield 1958; Fay 1982). Size dimorphism was significant in adult animals; adult males were approximately 1.14 times longer and 1.34 times heavier than adult females. Sexual size dimorphism in adults was achieved by a prolonged growth period and faster growth rate in males.

The breeding behavior of walruses has been described as either female defense polygyny (Sjare 1993) or lek-like

behavior (Fay et al. 1984). In polygynous pinnipeds, males generally mature at an older age than do females (Harrison 1969), which may reflect the extra time necessary to attain a body size large enough to successfully compete for access to females (Fay 1982). Sexual size dimorphism in polygynous pinnipeds has been attributed to intra-sexual competition for mates, where large body size in males is promoted through the ability to physically displace other males (Stirling 1983; Riedman 1989). Polygyny, and concomitantly dimorphism, tend to be reduced in ice-breeding pinnipeds (Stirling 1983; Riedman 1989). Stirling (1983), speculated that the selective pressures promoting dimorphism are reduced in ice-breeding species because suitable breeding substrate is not limited. Since females are not forced to group closely together, males are able to monopolize fewer females and intra-sexual competition for mates is reduced (Stirling 1983). However walruses which are ice-breeders, are highly gregarious and groups of estrus females hauled out onto pack ice elicit competitive behavior among breeding males. Attending males station themselves in the water near groups of females and perform elaborate vocal displays. Males form a dominance hierarchy competing for display stations primarily through acoustic and postural threat displays which occasionally lead to violent fighting (Fay et al. 1984; Sjare 1993).

"Lek-like" behavior implies a certain level of female choice. Fay et al. (1984) observed displaying Pacific walrus males stationed 7-10 meters apart and suggested that females could consort with the male of their choice within the display arena. Because females invest more heavily in offspring than do males, females should discriminate in their choice of mates (Darwin 1871). If the male traits that are attractive to females are directly or indirectly linked with large body size, inter-sexual selection operating through mate choice by females could be a selective force promoting large body size in males.

Irrespective of the forces promoting sexual dimorphism, the degree of dimorphism in walruses is generally less than in other polygynous pinniped species, suggesting that the selective mechanisms favoring dimorphism are not as strong (Fay et al. 1984).

The secondary growth-cycle of post-pubertal males, characteristic of a number of polygynous pinnipeds (McLaren 1993), was not evident in the present study. Fay (1982), described a secondary acceleration of growth in male Pacific walruses, however his conclusion was based upon fitting a line visually to cross-sectional age-length data. In a more quantitative analysis, McLaren (1993) reported that a combination of two fitted growth equations, describing

growth in sub-adult and adult male Pacific walruses respectively, produced slightly lower residual variance than a single function applied to males of all ages. However in the same study, McLaren could not justify using two equations to describe growth in male Atlantic walruses collected from Foxe Basin or Hudson Bay (see Mansfield 1958). Investigating changes in growth rates using crosssectional, age-at-length data is confounded by individual variability in body length. Detecting small shifts in postpubertal growth rates might be better accomplished using longitudinal size-at-age data from captive-reared specimens.

Mass-Length relationships

An assessment of body mass is a prerequisite for evaluating energy budgets and physiological rates of an organism (Calder 1982). For large marine mammals such as walruses, it is often difficult to obtain direct measurements of mass. In such instances, mass is usually approximated as a function of length to the third power (Laws 1959; McLaren 1993), or estimated from prediction equations based on linear measurements (see Laws 1959; Innes et al. 1981; Knutsen and Born 1991).

In this study, standard length proved to be the best explanatory variable for predicting the body mass of sampled walruses. The predicted values of body mass for Foxe Basin

walruses were significantly lower than estimates produced by the isomorphic equation generated for Atlantic walruses from Greenland (Knutsen and Born 1991). For a given length, Foxe Basin walruses were thinner than those from Greenland. The differences between the two equations may reflect seasonal variation, or true allometric differences between stocks. Pinnipeds exhibit considerable individual and seasonal variation in blubber stores and concomitantly in body mass (Lavigne et al. 1982). Mass-length differences between the two studies may be a function of the earlier collection dates in Greenland; in late May and early June, compared to late July and early August in Foxe Basin. Although seasonal fluctuations in body mass in walruses are poorly understood, Inuit hunters report that Foxe Basin walrus are leanest during the summer months. Given the propensity of pinnipeds to gain or lose weight according to their reproductive and nutritional status, predictions of mass from linear body measurements should not replace weighing individuals whenever possible (Innes et al. 1981).

Differences in the mass-length relationships of the two stocks may also reflect differences in population status relative to the availability of food resources. Although the status of Canadian and Greenlandic walrus stocks is poorly known (Richard and Campbell 1988; Born 1990), the relatively lean condition of Foxe Basin walruses could indicate that the Foxe Basin walrus stock is nutritionally

stressed. This hypothesis is addressed further in the general discussion.

Comparisons with other studies

Intraspecific comparisons have shown that population density relative to the availability of food resources can affect growth and maturation rates (Laws 1956; Sergeant 1973; Bowen et al. 1981; Boyce 1981; Innes et al. 1981). Growth curve parameters can therefore be a useful index for examining intraspecific differences in population status.

Because body mass is subject to non-heritable seasonal variation in relation to reproductive and nutritional status, standard length is a more useful measurement for comparative purposes. Comparison of growth curve parameters for Foxe Basin walruses with values reported by other studies indicated that: i) the growth patterns of male Foxe Basin walrus sampled in the 1980-90's and those sampled in the 1950's were similar; ii) Foxe Basin walruses sampled in the 1980-90's were significantly larger than walruses sampled from Hudson Bay in the 1950's; iii) although the Pacific walrus is generally considered the larger of the two subspecies (Mansfield 1958; Fay 1982), Foxe Basin walruses were as long, and in the case of females, longer than Alaskan walruses sampled in the 1970's. These results are discussed in the context of population status in the general discussion.

Part II

Reproductive biology of Atlantic walruses (Odobenus rosmarus rosmarus) in Foxe Basin, Northwest Territories, Canada

Introduction

Knowledge of an organism's reproductive biology and breeding cycles is essential to understanding its life history strategies and population dynamics (Boyce 1988). For wild pinnipeds, such information has usually been obtained through examination of reproductive material collected from harvested specimens (Mansfield 1958; Harrison 1969; Born 1980; Fay 1982; Boyd 1983).

For males, the presence of spermatozoa in the testes or epididymis is the most reliable index of potency (Mansfield 1958; Smith 1973; Fay 1982; Griffiths 1984a, 1984b). Most pinnipeds are seasonal breeders (Harrison 1969) and testes sampled outside of the breeding season are often quiescent. In several species, accelerated growth of the testes occurs with the attainment of sexual maturity. In such instances, testes size may provide indirect evidence of sexual maturity in the male (Fisher 1954; Laws 1956; Smith 1973).

Evidence of sexual maturity in the female (ovulation) is the presence of a *corpus luteum* or *corpus albicans* (Harrison and Weir 1977). In some mammalian species, *corpora albicantia* are retained in the ovaries for several years and have been used as indicators of reproductive history (Harrison 1969; Born 1980; Boyd 1983). Breeding

maturity (pregnancy) is indicated by the presence of a fetus or placental scars in the uterine horns (Harrison 1969; Working Group 7 1993).

Information on the reproductive biology of the Atlantic walrus (Odobenus rosmarus rosmarus) is limited. Mansfield (1958) reported that males attain sexual maturity at 6-7 years of age and that females ovulate for the first time between the ages of 5 and 10 years. He observed that female reproductive tracts collected in August carried small fetuses while one female collected in late May carried a full-term fetus. Based on the assumption that breeding occurred in May and June, Mansfield concluded that fetal development was direct and that gestation lasted approximately 380 days. More recent evidence has shown that Atlantic walruses breed primarily in February and March (Sjare 1993), suggesting that a period of embryonic diapause, characteristic of the Pacific subspecies (divergens), also occurs in the Atlantic walrus.

This study investigates the reproductive biology of Atlantic walruses from northern Foxe Basin. I describe changes in the reproductive organs which occur in association with age and reproductive maturity. The ages of sexual and breeding maturity are investigated and reproductive rates of mature females described. Fetal

morphology is used to describe prenatal growth and to estimate the date of implantation. Biases in sample collection which may preclude extrapolation of these data to the natural population are addressed.

Materials and Methods

Sample collection

Samples were collected primarily in July and August of 1988 and 1991-1993, from walruses harvested by Inuit hunters in northern Foxe Basin, NT, Canada, approximately 69°N, 80°W (see Fig. 1.1). Additional samples were collected from 9 males and 3 females in October-December of 1993.

For each animal, the reproductive organs and the mandible were collected and dates and locations of sampling recorded. Mother-calf pairs were identified when possible and the age and gender of each calf recorded. For males, the testes and epididymis were collected and identified as left or right. For females, the ovaries and uterus were collected with the broad ligaments and bladder left attached for orientation. Reproductive organs were stored frozen or in 10% buffered formalin. All reproductive material stored frozen was thawed and fixed in formalin for a minimum of three weeks prior to examination (Working Group 7 1993).

Mandibles were stored frozen until the teeth were removed for age analysis. Age estimates were made by counting annual incremental layers (growth layer groups:GLG's) in the cementum of the lower canine tooth (Garlich-Miller et al. 1993).

Males

The length and maximum diameter of each testis was determined to the nearest millimetre and the mass of the testis (less epididymis) was determined to the nearest gram (Fay 1982). The volume of each testis was measured to the nearest 10 ml by volumetric displacement of water. Previously frozen samples precluded histological investigation. Preliminary examination of fixed-never frozen testes indicated that even these samples were too poorly preserved to permit histological analysis.

After testing for differences between left and right testes (paired t-test), the mean measurements of each pair were calculated (Fay 1982). Of the four measurements recorded, mass had the highest measurement precision and was selected to describe testis growth. During the breeding season the testes of mature Pacific walruses increase in mass by approximately 40 % (Fay 1982). To account for this seasonal change in testes mass, analysis was restricted to July-August samples.

Non-linear least-squares procedures (SAS Institute Inc., 1985) were used to fit a von Bertalanffy growth equation (von Bertalanffy 1957) to age-related testis mass data. Richards and Gompertz growth functions were rejected in preliminary trials when they failed to meet convergence criteria. The equation used to describe testis growth was: $M_t = A(1-e^{-k(t-to)})$

where M_t is mean testis mass (g) at age = t, A is asymptotic mass, k and t_o are fitted constants and e is the base of natural logarithms (~ 2.71828183). The relationship between testis mass and volume was described by least-squares linear regression. The relationship between testis mass and linear measurements of length and diameter was examined with multiple regression analysis using \log_{10} -transformed data.

In the absence of histological data, the relationship between body size and testis mass was examined for abrupt changes which might indicate the onset of potency (Shirakihara et al. 1993). The cubed root testis mass was used as an index of testis size relative to standard body length. The equation relating testis mass to standard body length was:

 $(M)^{1/3} = a + b(length)$

where M is mean testis mass (g), length is standard body length (cm), a is the intercept and b is the coefficient associated with length. The distribution of the residuals around the least-squares regression line was examined visually for patterns, and tested for a normal distribution.

Females

Ovaries were detached from the uterus, trimmed of bursae and connective tissue and examined for ovulation scars. Ovaries were sectioned longitudinally at 2-3 mm intervals with a scalpel, leaving the sections attached at the base of the ovary to retain their relative positions. The surfaces of each section were examined to identify various ovarian structures. The maximum diameter of the largest follicle in each ovary was measured in one plane (mm) (Fay 1982). Corpora lutea were identified by their yellow-rouge color and rubbery texture. Corpora albicantia were white and had a hard fibrous texture. The maximum diameter of each corpus luteum and corpus albicans was measured (mm) in three orthogonal planes and the mean of these measurements used as an index of corpus size (Boyd 1984). When the outer edge of a corpus was concealed within a section, that diameter was estimated ± 2 mm. The extent of fibrosis in each corpus was also noted.

The arc-length of each uterine horn was measured (cm) along the anterolateral surface between the site of ovarian attachment and the junction of the two horns. The maximum diameter of each horn at its midpoint was also measured (cm). Each horn was opened longitudinally through the lumen and examined for placental scars and fetuses. The maximum width (mm) of placental scars was recorded (Working Group 7 1993).

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The reproductive status of sampled females was determined through examination of various indicators of reproductive history. A corpus luteum was considered evidence of ovulation in the current reproductive cycle (Harrison and Wier 1977). Corpora albicantia indicated ovulations in previous reproductive cycles (Mansfield 1958; Harrison 1969; Stirling 1973; Born 1980; Fay 1982; Boyd 1983). The presence of a fetus or a nidation chamber in the uterus were the criteria for pregnancy (Fay 1982; Working Group 7 1993). Previous pregnancies were indicated by enlarged uterine horns and placental scars of the uterine lining (Stirling 1973; Born 1980; Fay 1982; Working Group 7 1993).

When mother-calf pairs were identified, the age of the calf was used to estimate the age of the most recent placental scar and *corpus albicans* (Fay 1982). Since calves are normally weaned by the age of 2-3 years (Mansfield 1958; Miller and Boness 1983; Fisher 1989), only newborn and yearling calves were considered. The size and structure of placental scars and *corpora albicantia* in this subset were used to estimate the age of the most recent placental scar and *corpus albicans* for those animals for which mother-calf relationships were not identified.

Females with ovaries showing no signs of prior ovulations are referred to as immature (Working Group 7 1993). Females with ovaries containing at least one corpus luteum or corpus albicans were regarded as sexually mature. (Working Group 7 1993). Females with ovaries containing a corpus luteum (ovulated in current cycle) are referred to as ovulated and those without a corpus luteum are referred to as un-ovulated. Sexually mature females with uterine horns showing evidence of past or present pregnancies were considered to have reached breeding maturity (Fay 1982). Females with an identifiable fetus or nidation chamber in the uterus are referred to as pregnant. Females that had given birth 1-2 months prior to collection are referred to as postpartum while those that had given birth in the previous reproductive cycle are referred to as 1-year postpartum.

Follicles, corpora lutea and corpora albicantia were compared with parametric statistics. Accumulation of corpora albicantia in the ovaries with age was described with linear regression. Chi-square frequency analysis was used to determine if successive ovulations occurred from the same or opposite ovary.

To describe growth of the uterus, only non-pregnant and non-parturient animals were considered (Fay 1982). After

testing for differences between left and right uterine horns (paired t-test), the average length and diameter of both uterine horns of each animal were used to describe growth. To account for changes in uterine morphology associated with breeding maturity (Working Group 7 1993), linear regression models were used to examine uterine growth in immature and previously parous animals, respectively. Differences in uterine morphology between various reproductive classes were described with t-tests for unequal sample sizes (Glantz 1992).

The minimum ages of sexual maturity and breeding maturity were determined from evidence of recent reproductive history and derived age estimates. Agespecific reproductive data were insufficient to estimate the average age of sexual and breeding maturity (DeMaster 1978). Chi-square frequency analysis was used to investigate agerelated differences in reproductive rates and to test observed ovulation, pregnancy and birth rates against biennial and triennial models. The effect of previous reproductive success on the likelihood of ovulation and conception in the current cycle was investigated for females for which the reproductive history in the last two breeding cycles could be determined.

Fetuses

For each fetus, the horn of pregnancy, crown-rump length (mm), mass (± 0.1 g) and gender were recorded (Working Group 7 1993). The null hypotheses that: *i*) the fetal sex ratio is 1:1, and *ii*) the sex ratio of calves is 1:1., were tested with Chi-square frequency analysis.

Fetal growth was described using least-squares regression models where crown-rump length and the cube root of fetal mass were examined as functions of collection date (Frazer and Huggett 1974; Stewart *et al.* 1989). As the ability to generate a meaningful prediction equation for fetal growth was limited by a small sample size and short period of collection, previously reported data (Mansfield 1958) for 11 Atlantic walrus fetuses were included to generate an average model of fetal growth.

The onset of active gestation was estimated from the xon y regressions of time in relation to fetal length and mass (g)^{1/3} (Stewart *et al.* 1989). The walrus blastocyst experiences negligible growth prior to implantation (Fay 1982), reaching a maximum size of approximately 7 mm (Burns (unpublished data) *cited in* Fay 1982). Implantation is followed by active embryonic growth which is approximately linear (interpreted from Fig.118 *in* Fay 1982). If implantation coincides with the onset of active gestation the *x*-intercept of the inverse regression of fetal growth should approximate the mean date of implantation.
Results

The reproductive organs of 99 male and 79 female walruses were examined. Sample sizes for different analyses varied according to the availability of ageing structures and reproductive material.

Males

Although testes were usually slightly unequal in size, significant differences between right and left testes were not apparent in length, maximum diameter, mass or volume (Table 2.1). Measurements used to describe testis growth are the means for each pair of testes, or a single testis when both were not available. Testes attained an asymptotic mass of 445.20 g ($R^2 = 0.68$, F = 627, n = 89) (Fig. 2.1). Testis mass (g) scaled with testis volume (ml) according to the simple linear regression equation:

$$M = 5.98 + 1.02$$
 (volume) $R^2 = 0.99$, $F_{1,87} = 999.99$

The predictive equation relating testis mass (g) to linear measurements of length (mm) and diameter (mm) was:

 $log_{10}mass = -2.31 + 1.28(log_{10}length) + 1.09(log_{10}diameter)$

$$(R^2 = 0.91, F_{282} = 435.56)$$

Table 2.1. Bilateral symmetry of Atlantic walrus (Odobenus rosmarus rosmarus) testes.

Measurement	Left X ± sd	Right x ± <i>sd</i>	Test t, df	
Testis:				
Length (mm)	167.9 ± 34.5	167.1 ± 37.8	0.10 ^{ns} , 68	
Max. diameter (mm)	56.7 ± 14.5	58.3 ± 12.4	0.48 ^{ns} , 68	
Mass (g)	321.6 ± 119.8	316.2 ± 113.7	0.19 ^{ns} , 72	
Volume (ml)	303 ± 109	309 ± 117	0.19 ^{ns} , 70	

^{ns} P > 0.05.

Figure 2.1. Testis growth in Atlantic walruses (*Odobenus rosmarus rosmarus*) as a function of age (t). Each point represents the mean value of the pair from one specimen, or, a single testis when both were not available (n = 89). The curve was fitted according to a von Bertalanffy growth equation.



The relationship between body size and testis mass^{1/3} did not provide the criterion necessary for distinguishing between sexually mature and immature males. The equation relating testis mass^{1/3} to standard body length scaled linearly ($R^2 = 0.72$, $F_{1,76} = 198.14$) and the residuals were normally distributed (P > 0.05) around the regression line (Fig. 2.2). Testes collected in December tended to be heavier at a given body length than those sampled in July and August, but were not analyzed statistically due to the small sample size.

Females

Fifteen of the 79 female reproductive tracts examined were immature. Three of the immature samples consisted of ovaries only. The ages of immature females ranged from 0 (young of the year) to 6 years. Age estimates for 64 sexually mature females ranged from 6 to 26 years. Ageing structures were not available for 5 mature females.

Thirty three (51.6 %) of the mature females had ovulated in the most recent cycle but only 21 (32.8 %) showed signs of pregnancy. One 7-year-old animal and two 12-year-old animals were pregnant for the first time. All of the other sexually mature reproductive tracts carried evidence of previous pregnancies (ages 6-26).

Figure 2.2. The relationship between body length (cm) and the cubed root of testis mass (g) in 77 male Atlantic walruses (Odobenus rosmarus rosmarus). Each point represents the mean value of a pair of testes, or a single testis when both were not available. Open circles and the linear regression line represent animals sampled in July and August. Solid circles represent animals sampled in December and are not included in the regression analysis.



Nineteen (29.7 %) of the mature reproductive tracts carried evidence of recent parturition, including that of one 6-year-old female. Newly formed *corpora lutea* were not found in any of these recently postpartum specimens. Seventeen (26.6 %) of the mature females were diagnosed as 1-year post partum. Of these, 7 (41.2 %) had ovulated in the most recent cycle and 5 (29.41 %) were newly pregnant.

Follicles appeared as spherical, fluid-filled vesicles distributed in the ovarian cortex just beneath the tunic. The ovaries of newborn calves contained no macroscopically visible follicles. Follicles in immature females 1-6 years of age ranged from 1 to 5 mm in maximum diameter. In sexually mature animals, follicles ranged from 1 to 27 mm in maximum diameter.

Corpora lutea were round to oval in shape and ranged in diameter from 10.3 to 34 mm ($\bar{x} = 26.20$ mm, sd = 4.14, n =32). An ovulation scar in the ovarian tunic was observed in 10 (30.3 %) of the ovulated specimens. There was a small but significant difference in the mean size of corpora lutea associated with an identifiable fetus ($\bar{x} = 27.6$ mm, sd = 2.9, n = 20) and those without ($\bar{x} = 23.9$ mm, sd = 5.3, n = 12, t = 2.58, df = 30, P < 0.05). All corpora lutea contained variable amounts of connective tissue septae and the degree of fibrous intrusion did not appear to be related to the

presence or absence of a fetus. A corpus luteum occurred most frequently in the ovary opposite the ovary with the largest corpus albicans (n = 20) than from the same one (n = 8: $X^2 = 5.14$, P < 0.05).

Compound and accessory corpora lutea were found in the ovaries of three animals. In one, the right ovary contained a compound corpus luteum composed of a 14.3 mm and a 10.3 mm follicle. The smaller follicle was incompletely luteinized and had a central cavity 3 mm in diameter. In the two other specimens, several small luteinized follicles (2-9 mm) were present in the ovary opposite the ovary containing a normal corpus luteum.

Corpora albicantia appeared as white, irregularly shaped fibrous scars ranging in mean diameter from 1 to 27.7 mm. The largest corpora albicantia found in the ovaries of postpartum females ranged from 17.7 to 27.7 mm in mean diameter ($\bar{x} = 22.8$ mm, sd = 2.6, n = 17). These were significantly larger (t = 5.81, df = 31, P < 0.05) than the largest corpora albicantia found in 1-year postpartum females, which ranged from 10.7 to 24.7 mm in diameter ($\bar{x} = 16.4$ mm, sd = 3.7, n = 16).

The number of corpora albicantia found in the ovaries of sexually mature females increased with age at an average rate of 0.25 per year ($R^2 = 0.54$, $F_{1,58} = 66.90$) (Fig. 2.3).

Figure 2.3. Accumulation of corpora albicantia in the ovaries of the Atlantic walrus (Odobenus rosmarus rosmarus) as a function of age. Each point represents the total number of corpora albicantia in both ovaries of one female. Open circles represent immature animals, solid circles and fitted least-squares regression line represent mature animals.



In 64 % of mature females, the number of *corpora lutea* and *corpora albicantia* found in the right and left ovaries were identical or differed by only one, consistent with a pattern of alternating ovulations.

Although uterine horns of non-pregnant, non-parturient females were often unequal in size, there was no statistical difference in the average length or maximum diameter of left and right horns (Table 2.2). In the subset of immature females, there was a significant and positive relationship between age and uterine horns length ($R^2 = 0.45$, $F_{1,10} = 8.06$) and between age and uterine horn diameter ($R^2 = 0.68$, $F_{1,10} = 21.14$) (Fig. 2.4). In non-pregnant, non-parturient females that had attained breeding maturity, there was no detectable relationship between uterine size and age (length: $R^2 = 0.11$, $F_{1,17} = 2.07$; diameter: $R^2 = 0.04$, $F_{1,17} = 0.61$). These uterine horns ranged from 14 to 30 cm in length ($\bar{x} = 21.62$ cm, sd = 3.63, n = 18) and from 4.25 to 7.5 cm in maximum diameter ($\bar{x} = 5.84$ cm, sd = 0.81, n = 18).

The uterine horns of mature females that were not pregnant and had not recently given birth were longer (t = 9.38, df = 33, P < 0.05), and wider (t = 13.14, df = 33, P < 0.05) than immature horns (Table 2.3).

Table 2.2. Bilateral symmetry of non-pregnant, non-parturient uterine horns in the Atlantic walrus (Odobenus rosmarus rosmarus).

Measurement	Left x ± sd	Right $\bar{x} \pm sd$	Test t, df
Uterine horn			
Length (cm)	17.1 ± 7.3	17.5 ± 7.7	0.20*, 64
Max. diameter (cm)	4.1 ± 2.3	4.3 ± 2.4	0.31*, 64
Length (cm) Max. diameter (cm)	17.1 ± 7.3 4.1 ± 2.3	17.5 ± 7.7 4.3 ± 2.4	0.20 [*] , 0.31 [*] ,

* P > 0.05.

Figure 2.4. Length (A) and diameter (B) of nonpregnant, non-parturient uterine horns of 31 Atlantic walruses (Odobenus rosmarus rosmarus). Each point represents the mean value of the pair from one female. Open circles represent immature animals, solid circles mature specimens. Least-squares regression lines were fitted to measurements of immature uterine horns.



Reproductive Length (cm) _____Width (cm) Status n Range $ar{\mathbf{x}} \pm sd$ Range $\bar{\mathbf{x}} \pm sd$ Immature^a 12 5-15 8.87 ± 3.09 1-1.9 1.40 ± 0.28 <u>Mature</u> Quiescent^a 23 14-30 21.55 ± 4.10 2.5-7.5 5.43 ± 1.21 Pregnant 19 Preg. horn 24-96 37.34 ± 15.75 4-22 7.73 ± 3.79 Other horn 21-40 28.13 ± 4.83 3.5-9 5.49 ± 1.49 <u>Postpartum</u> 18 P.p. horn 19-35 25.56 ± 3.96 6.5-12 7.78 ± 1.37 Other horn 11-27 20.00 ± 3.75 4.5-8 6.19 ± 1.06

^a Average measurements of both uterine horns. Quiescent: non-pregnant and non-parturient in most recent reproductive cycle.

P.p: Postpartum

Table 2.3. Size of the uterine horns of Atlantic walruses (Odobenus rosmarus rosmarus) in relation to reproductive status.

In pregnant reproductive tracts, the horn of pregnancy was always associated with the ovary containing the *corpus luteum* and was significantly longer (t = 2.44, df = 36, P < 0.05), and wider (t = 2.40, df = 36, P < 0.05) than the non-gravid horn (Table 2.3). Fetuses were found with equal frequency in left (n = 10) and right (n = 10) uterine horns. In 5 pregnant, 1-year postpartum females, the fetus was in the horn opposite the horn of previous pregnancy 4 times and in the same horn once.

Involution of the uterus was still incomplete at 1-2 months postpartum. Postpartum horns were significantly longer (t = 4.34, df = 34, P < 0.05) and wider (t = 3.87, df = 34, P < 0.05) than inactive horns (Table 2.3).

The lumen of non-gravid, non-parturient horns was tightly constricted and the uterine lining (endometrium) was arranged in a series of sharply ridged longitudinal folds 3-5 mm in depth (Fig. 2.5 A). In gravid horns the endometrial lining was distended and greatly reduced in thickness at the site of implantation (Fig. 2.5 B). The lumen of postpartum horns was dilated (7-15 mm) and the endometrium bore incompletely healed placental scars 27-65 mm in width ($\bar{x} = 43.68 \text{ mm}$, sd = 10.08, n = 19) (Fig. 2.5 C). In 1-year postpartum females, the uterine lumen was constricted and placental scars ranged from 19-38 mm in

Figure 2.5. The lining of the uterine horns of Atlantic walruses (*Odobenus rosmarus rosmarus*) in relation to reproductive status.

(A) Uterine horns and ovaries of a female young of the year(lateral dissection, ventral view). Note sharply ridgedlongitudinal folds of the endometrium (arrow).

(B) Gravid horn with fetus (right horn, lateral dissection ventral view). Note reduced thickness of the endometrium at the site of implantation (arrow).



Figure 2.5. ..cont'd

(C) Recently postpartum uterine horn (right horn, lateral dissection, ventral view). Note dilated lumen and incompletely healed placental scar (PS).

(D) One year postpartum horn (right horn, longitudinal bisection). Note constricted lumen and reduced size of placental scar (PS) relative to Fig. 2.5 C.



width ($\bar{x} = 26.82 \text{ mm}$, sd = 5.92, n = 17). These placental scars were significantly smaller than those of recently postpartum specimens (t = -6.02, df = 34) (Fig. 2.5 D). The age of placental scars older than one year could not be determined with any degree of certainty. These scars ranged from 9 to 22 mm in width ($\bar{x} = 14.86 \text{ mm}$, sd = 4.25, n = 23).

Anomalies and pathologies

The reproductive tract of one 5-year-old female was under-developed (Fig. 2.6 A). The unopened tract was similar in size and shape to that of a newborn calf. Dissection revealed that the left uterine horn was not canalized.

A failed pregnancy was found in the right uterine horn of an 18-year-old female (Fig. 2.6 B). The horn contained three atria 35-56 mm in diameter, filled with a soft opaque gel. The largest of the three atria contained a solid fleshy nodule attached to the wall of the uterus. There was a large *corpus albicans* in the right ovary.

A large (10.4 cm) cervical cyst was found in the reproductive tract of a mature female for which there was no ageing material (Fig. 2.6 C). The cyst was encapsulated by several layers of tissue and filled with a light brown purulent fluid. Ectopic cervical pregnancy was ruled out by evidence of recent placentation in the right uterine horn. Figure 2.6. Anomalies and pathologies of the female reproductive tract in 3 Atlantic walruses (Odobenus rosmarus rosmarus).

(A) Occluded uterine horn in a 5-year-old animal(longitudinal dissection, dorsal view). The left uterinehorn was not canalized. Dotted line outlines position oflumen in the right horn prior to dissection.

(B) Failed pregnancy in the right uterine horn of a 18year-old female (longitudinal bisection). The right ovary contained a *corpus albicans* 23.6 mm in diameter.

(C) A 10.4 cm cervical cyst in a mature female (longitudinal dissection, ventral view). The cyst was filled with a light brown purulent fluid prior to dissection.



Sexual and breeding maturity

None of the animals examined had ovulated for the first time in the most recent reproductive cycle. The reproductive organs of 14 specimens less than 5 years of age and one 6-year-old animal were immature. A recently postpartum 6-year-old animal was estimated to have ovulated for the first time at the age of 5 years. The reproductive organs of all females aged 7 years or older carried evidence of prior ovulation. Ageing structures were not available for 5 mature females.

Three females were pregnant for the first time and one had recently given birth to her first calf. The estimated age of first pregnancy in these 4 animals ranged from 5 to 12 years (Table 2.4). All other mature animals examined were previously parous.

Reproductive rates

Small sample sizes for some year-classes violated the statistical requirements for chi-square analysis and precluded the calculation of meaningful age-specific reproductive rates. There was no significant difference in the frequency of ovulations, pregnancies or presumed births between the 32 youngest mature animals (6-12 years) and the 27 oldest animals (13-26 years) ($X^2_{\text{ov}} = 1.42$, $X^2_{\text{preg}} = 0.26$, $X^2_{\text{p.p.}} = 2.78$, P > 0.05) (Table 2.5).

Table 2.4. Estimated age of first pregnancy in four Atlantic walruses (Odobenus rosmarus rosmarus).

Sample #	Sample Date	Age	Reproductive status	Est. age of 1st pregnancy
IG88-73	21/07/88	6	Postpartum	5
W91-34	15/07/91	7	Pregnant	7*
HB88-17	22/07/88	12	Pregnant	12*
IG88-60	16/07/88	12	Pregnant	12*

*Samples were diagnosed as primiparous based upon uterine horn morphology.

Table 2.5. Number and frequency of female Atlantic walruses (*Odobenus rosmarus rosmarus*) which had ovulated, were pregnant, or had recently given birth.

Age (years)	Ovulated	Pregnant	Postpartum	sum [*]
6-12	14 (0.44)	12 (0.37)	12 (0.37)	32
13-26	18 (0.67)	8 (0.30)	4 (0.15)	27
Unknown	1 (0.20)	1 (0.20)	3 (0.60)	5
All ages	33 (0.52)	21 (0.33)	19 (0.30)	65

* Females may be represented in more than one category.

The ovulation frequency (0.52) of all 64 mature females was not significantly different from a model of biennial ovulation $(P_{ov} = 0.5)$ ($X^2 = 0.06$, P > 0.05) but significantly different from a model of ovulation once every three years ($P_{ov} = 0.33$) ($X^2 = 9.56$, P < 0.05). Ovulation had not occurred in any of 19 recently postpartum females. In 17 1-year postpartum females, the frequency of ovulation was 0.41. In 28 females that had not given birth over the last two breeding cycles, the frequency of ovulation was 0.93.

Pregnancy occurred in 12 (33 %) of the 64 mature walruses. The observed frequency of pregnancies was significantly different from a model of biennial pregnancies ($P_{Preg} = 0.5$) ($X^2 = 7.56$, P < 0.05) but not significantly different from a model of pregnancy every three years ($P_{Preg} = 0.33$) ($X^2 = 0.01$, P > 0.05). Pregnancies were not observed in 19 recently postpartum specimens. Of 17 1-year post partum females, 5 (29 %) were newly pregnant. In 28 sexually mature females that had not given birth in the past two years, the frequency of pregnancy was 0.57.

Nineteen of 64 mature walruses were recently postpartum. The proportion of postpartum specimens (0.30) was significantly different from a model of biennial births ($P_{p,P.} = 0.5$) ($X^2 = 10.56$ P < 0.05) but not significantly different from a model of one birth every three years ($P_{p,P.} = 0.33$) ($X^2 = 0.38$, P > 0.05). In recently postpartum reproductive tracts, the ability to estimate

calf production was limited to the most recent cycle because the large, recent placental scar masked all previous scars.

Fetuses

Of the 33 females which had ovulated in the most recent cycle, 20 carried a fetus. One other female that had a *corpus luteum* and a nidation chamber, but no visible embryo, was also presumed to be pregnant. No un-implanted embryos were found.

The sex ratio of 17 fetuses for which gender could be determined did not differ significantly from 1:1 (10 males:7 females, $X^2 = 0.53$, P > 0.05). A sex ratio of 1:1 was also observed in 14 newborn calves (7 males:7 females).

Fetuses ranged from 16 mm to 42.2 cm in crown-rump length and from 1 g to 6.05 kg in mass. Fetuses increased 0.29 cm * d⁻¹ in crown-rump length and 0.12 g^{1/3} * d⁻¹ in mass over the range of collection dates (Table 2.6; Fig. 2.7). Approximations of implantation dates based on the inverse regressions of fetal growth ranged from day 178 to 184 (June 29 to July 3) (Table 2.7).

Table 2.6. Fetal growth of Atlantic walruses (Odobenus rosmarus rosmarus) as a function of collection date^a.

Variable	n	Slope	Intercept	R ²	F	Р
Crown-rump length, cm	20 ^b	0.29	-51.67	0.95	342.24	*
Mass, g ^{1/3}	20 ^b	0.12	-21.95	0.96	445.84	*
Crown-rump length, cm	32 ^c	0.33	-60.44	0.99	999.99	*
Mass, g ^{1/3}	21 ^c	0.12	-20.64	0.99	999.99	*

^a Day of year; where January 1st equals day 1 and day 366 of a biennial reproductive cycle.

^b This study.

^c Pooled data; this study and Mansfield (1958).

* P < 0.05.

Table 2.7. Predicted date of implantation (x-intercept) based on the inverse of regressions from Table 2.6.

Variable date	n S	Slope	Intercept ^a	SEI	Calendar
Crown-rump length, cm	20 ^b	0.33	181	6.66	June 30
Mass, g ^{1/3}	20 ^b	7.85	180	5.87	June 29
Crown-rump length, cm	32°	0.31	184	6.69	July 3
Mass, g ^{1/3}	21 ^c	8.55	178	6.36	June 27
Mean			181		June 30

 ${\rm SE}_{\rm I}$ Standard error of the Intercept.

Figure 2.7. Fetal growth of the Atlantic walrus (Odobenus rosmarus rosmarus). (A) Crown-rump length (cm) as a function of collection date. (B) Mass (g)^{1/3} as a function of collection date. Calendar days were converted to days of the year, where day 1 and day 366 represent January 1 in two consecutive calendar years. Open circles represent fetuses collected in the present study, solid circles represent data from Mansfield (1958). Lines were fit according to least-squares linear regression.



Discussion

Sampling biases and limitations

The data presented in this study were obtained from harvested specimens and do not represent a random sample. Biases associated with the harvest which include hunter selection as well as the behavior and distribution of the animals, introduce error into estimates of reproductive rates.

Young and old year classes were poorly represented in the collection, making calculations of age-specific reproductive rates impossible. In the Pacific walrus, reproductive rates decline with age (Fay 1982). Mansfield (1958) found "several old barren females" in his collection of Atlantic walruses from Foxe Basin. Given that most of the mature animals examined in the present study were young adults, reproductive rates are likely biased towards the most productive class of females. Furthermore, several hunters in both communities expressed a preference for hunting mother-calf pairs which could result in over-estimation of the rate of calf production and bias the age of reproductive maturity towards younger age classes.

Males

Age-related growth of the testes was best described by a non-linear growth model. Although the von Bertalanffy growth equation explained most of the observed variation in testes mass,

the model under-estimated testes size in newborn calves. At birth, enlarged testes is characteristic of several pinniped species. During the third trimester of pregnancy, steroid hormones from the mother result in the formation of large masses of interstitial tissue in fetal testes (Harrison 1969). A larger sample size and histological examination of 1 to 4-year-old males are required to assess the degree of hypertrophic testicular development in walrus calves and to improve the characterization of testes growth in juvenile males.

Although the sample size was too small for meaningful statistical comparisons, testes sampled in December tended to be heavier those sampled in July and August. This is consistent with Fays' (1982), observation that during the breeding season the testes of sexually mature male Pacific walrus increase in mass by approximately 40 %.

Fay (1982) reported that the period of potency in adolescent males occurs 1-2 months later than in fully mature adults. In the present study, there was considerable variation in testes size at all ages. However, the testes of the oldest individuals tended to be smaller than those of intermediate age classes. This may reflect an age-related difference in the seasonal development of the testes, with the oldest animals representing a more advanced stage of retrogression. Samples collected over a broader range of collection dates are required to test this hypothesis.

In some polygynous species, testes attain asymptotic size at sexual maturity, while continued post-pubertal somatic growth favors the ability of the older (larger) males to compete for access to estrus females (Kenagy and Trombulak 1986). Accelerated testicular growth has been correlated with sexual maturity in a number of pinniped species including southern elephant seal (Mirounga leonina) (Laws 1956), ringed seal (Phoca hispida) (Smith 1973) and harp seal (Phoca groenlandica) (Fisher 1954). I found no criterion for distinguishing between immature and sexually mature male walruses on the basis of testes size. Testes and somatic growth scaled linearly, without a inflection point which might indicate the minimum body size associated with potency. However, the absence of a noticeable shift in testicular growth pattern may have been because most of the testes examined were collected from walruses sampled outside of the breeding season, and were likely non-spermiogenetic. Testes sampled during the breeding season are required to test this hypothesis.

Females

The female walrus reproductive tract experiences very little growth until the attainment of sexual maturity (Fay 1982). In sexually mature females, cyclic changes occur in the ovaries and uterine horns in relation to their function in the breeding cycle.

Macroscopically visible follicles were found in the ovaries of all animals older than 1 year of age. Most of the follicles observed were less than 5 mm in diameter. Fay (1982) observed follicles up to 5 mm in diameter in the ovaries of immature, anestrus and pregnant Pacific walruses, and concluded that they represented a resting stage, not related to pro-estrus.

Other investigators have considered follicles > 10 mm close to the size required for ovulation (Mansfield 1958; Fay 1982). In this study, follicles 12, 15, 20 and 27 mm in diameter were found in the ovaries of 4 un-ovulated, non-parturient females sampled in July. These follicles were all within the observed range of *corpora lutea* diameters (10-34 mm) and may have been close to ovulation. Follicular development in these specimens appeared to be out of phase with the other metestrus females which carried well developed *corpora lutea*. Given that males do not appear to be in breeding condition in July and August, ovulations occurring at this time are unlikely to result in conception.

A postpartum or lactational estrus is characteristic of most pinniped species (Harrison 1969; Smith 1973; Born 1980; Boyd 1983). Fay (1982) reported a phase of postpartum follicular activity in Pacific walruses, which peaked in July or August. In the present study, the ovaries of four postpartum females contained follicles 10, 10, 12 and 16 mm in diameter. However,
corpora lutea were not observed in any postpartum specimens. In walruses, the postpartum development of follicles does not appear to result in ovulation (Mansfield 1958; Fay 1982).

I found no morphological criteria for distinguishing between corpora lutea of successful pregnancies and those of infertile ovulations. Other investigators have found that a corpus luteum may persist for several months in absence of conception (pseudopregnancy) (Mansfield 1958; Harrison 1969; Fay 1982; Working Group 7 1993). In pregnant females, fibrous invasion of corpora had already begun in the early stages of gestation, and by 1-2 month postpartum they were completely filled with connective tissue.

In pinnipeds, ovulation from alternate ovaries has been attributed to the follicle-suppressing effects of the most recent *corpus luteum* (Harrison 1969; Stirling 1973; Born 1980; Boyd 1983). This alternating pattern of successive ovulations was apparent in most but not all of the specimens examined. Deviation from an alternating cycle may relate to the absence of a postpartum estrus. The follicle-suppressing effects of a corpus may be reduced after a year or more of regression preceding the next estrus cycle.

The age and rate of regression of corpora albicantia resulting from an infertile ovulation (i.e. without corroborating

evidence of parturition in the uterine horns) could not be determined with any degree of certainty. The broad range of *corpora albicantia* sizes suggests that regression continues over several years until they are no longer macroscopically visible. Although *corpora albicantia* tend to accumulate in the ovaries with age, a large variation in the number of *corpora albicantia* found in the ovaries of older specimens suggests that retention is variable.

Using of counts of corpora lutea and corpora albicantia to estimate reproductive frequency is suspect. The method is complicated by the possibilities of corpora lutea resulting from pseudo-pregnancies, the formation of accessory corpora and luteinized follicles, and by variable rates of corpora regression.

Uterine horn size has been used to estimate reproductive status for a number of pinniped species (Harrison 1969; Smith 1973; Born 1980). In walruses, morphological measurements of uterine horns have been used to distinguish between uterine horns that have never been pregnant (long and slender) and those that have previously supported a pregnancy (short and thick) (Working Group 7 1993). The immature horns examined in this study had a length:width ratio of approximately 6:1, while previously pregnant horns had a length:width ratio of approximately 4:1.

Parturition results in the formation of a prominent placental scar in the uterine lining. I found no criteria for determining the age of regressing placental scars beyond 2 years. Older placental scars are apparently obliterated by the most recent pregnancy, as each uterine horn contained a maximum of one visible placental scar. The variation in size of older placental scars suggests that they may be retained for several years, but it is not known how long placental scars normally persist in the uterus in absence of recurring pregnancies. Several mature specimens had no visible placental scars, suggesting that they eventually fade and disappear and indicating that reproductive rates may decline with age.

Anomalies and pathologies

Uterine anomalies and pathologies were observed in 3 female reproductive tracts. In ringed seals (*Phoca hispida*) of the northern Baltic Sea, a high incidence of uterine pathologies and *in utero* fetal mortalities has been attributed to high levels of environmental contaminants (Helle 1980). Direct evidence linking reproductive pathologies in walruses to environment contaminants is yet forthcoming. Contaminant studies of Foxe Basin walrus tissues have indicated low levels of organochlorine pesticide residues and PCB's relative to other locations throughout the Arctic (Wagemann *et al.* 1993). Although it is unlikely that these internal pathological conditions affected hunter selection biases, the size of the collection from which they were drawn was

too small to establish meaningful rates of pathologies and *in utero* fetal mortalities, or to assess their impact on the reproductive potential of the population.

Sexual and breeding maturity

The average ages of sexual and breeding maturity are sensitive indices of the status of a population (Laws 1956; Sergeant 1973; DeMaster 1978), but estimates of these statistics are dependent upon the availability of age-specific reproductive data. DeMaster (1978) suggests an age-specific sample size of > 25 to generate a meaningful estimate of variance for comparisons between populations. This sample size was not met in the present study.

In the present collection, the poor representation of juvenile and adolescent age classes made interpretation of the onset of maturity difficult. The limited available data suggest that ovulation is possible in 5 year old females. All females \geq 7 years of age had previously ovulated. However primiparous specimens up to 12 years of age indicate that ovulation does not always result in pregnancy and suggest that breeding maturity does not necessarily coincide with sexual maturity. Increased sample sizes of females between the ages of 4 and 12 years are required to determine the mean ages of sexual and breeding maturity in the Foxe Basin stock.

Reproductive rates

The walrus has the lowest known reproductive rate of any pinniped species (Fay 1982). Reproductive rates are constrained in one season as a result of reproductive acts in previous seasons. Although counts of *corpora albicantia* suggest that annual ovulations are possible, a pregnancy which lasts through the following breeding season lowers the minimum interval between successful births to 2 years. Most pinnipeds mate within days or weeks of parturition (Stirling 1983; Boyd 1991), but walruses give birth several months after the breeding season (Fay 1982) and are not known to have a postpartum estrus. Of the 1-year postpartum females, only 41 % had ovulated in the following reproductive cycle, indicating that fecundity is reduced in the breeding season following the birth of a calf.

The factors affecting the resumption of estrus cycles in walruses are unknown. In other mammals, estrus is suppressed during lactation by elevated levels of the pituitary hormone prolactin, which is produced and maintained in response to the suckling stimulus (Harrison 1969; Kiltie 1988; Boyd 1991). Atlantic walruses nurse calves for more than a year (Mansfield 1958, Miller and Boness 1983, Fisher 1989) and ovulation may be suppressed until the calf is weaned (Harrison 1969). This hypothesis is consistent with the observation that 93 % of females that have not given birth for two years had ovulated in the most recent cycle.

The frequency of pregnancies in mature females (0.33) suggests that the average calf production is approximately once every three years. This is similar to Mansfield's (1958) study which reported a pregnancy rate of 0.35 for 17 mature Atlantic walruses collected in Hudson Bay. Mansfield concluded that the reproductive cycle was essentially biennial but that missed pregnancies lowered the average calf production to once every three years.

Based on a collection of 206 mature female Pacific walruses sampled in the 1970's, Fay (1982) reported that in any given year approximately 40 % of sexually mature females conceive and 38 % produce a calf. Fay concluded that the difference between these two values represents the rate of *in utero* fetal mortality. These estimates for Pacific walruses are somewhat higher than the pregnancy and presumed birth rates observed in the present study. The differences between the two studies may reflect different sample collection biases or true differences in the reproductive rates of the respective populations. This hypothesis is considered in the context of population status in the general discussion.

Fetuses

Each pregnancy involved a single fetus although twin fetuses in walrus have occasionally been reported (Kibal'chich 1988; Fay et al. 1991). Fetuses were found with equal frequency in left

and right uterine horns, always ipsilateral with the ovary containing the *corpus luteum*. Indeed the possibility of transuterine migration of ova is unlikely given the absence of interluminal connections between uterine cornua (Fay 1982).

The sex ratio of fetuses and newborn calves was not significantly different from 1:1 as previously reported (Mansfield 1958; Fay 1982). Males may experience higher adult mortality rates than do females. Fay and Ray (1979) report that the sex ratio of adult Pacific walruses in the Bering Sea is approximately 1 male:3 females.

Fetal growth

In mammals, the duration of gestation is highly correlated with fetal size at birth (Martin and MacLarnon 1985; Harvey and Read 1988). The walrus neonate is the largest of all pinniped species and has the longest reported gestation period (Stewart 1983; Kovacs and Lavigne 1992). Unlike other pinniped species which give birth to and wean their calves in one location (Stirling 1983), the walrus neonate accompanies its mother from the time of birth for up to two years (Mansfield 1958; Miller and Boness 1983). This behavior is facilitated by a large precocial neonate (Stewart 1983; Kovacs and Lavigne 1992).

Linear least-squares regression models for fetal size as a function of collection date explained 96 % of the variation in

mass, and 95 % of the variation in fetal crown-rump length. These growth rates bore a close resemblance to fetal length-date data for the Pacific walrus (Fay 1982, Fig. 118) indicating similar growth rates and implantation dates for the two subspecies. Frazer and Huggett (1974) presented an estimated growth rate for Atlantic walrus fetuses of 0.09 $g^{1/3} * d^{-1}$ (based on Mansfield 1973), somewhat less than the fetal growth rate observed in this collection (0.12 $g^{1/3} * d^{-1}$). However, Frazer and Huggett's (1974) calculation assumed that delayed implantation did not occur in walruses, and that active gestation lasted for more than a year. More recent studies of the Pacific subspecies have shown that delayed implantation does occur and that active gestation is approximately 11 months in duration (Fay 1982).

Timing of implantation

All pinnipeds appear to have an obligate period of delayed implantation (Boyd 1991). Delayed implantation may be a phylogenetic artifact from an ancestral terrestrial carnivore line, which developed in response to seasonal variations of food and climate (Stirling 1983; Reppening 1976). This pre-adaptation allows females to disassociate the time of mating from the time of parturition and allows the neonate to be born at a time when conditions are optimal for survival (Boyd 1991). At high latitudes the season of birth for walruses (May and June) is characterized by solar radiation which is near its annual peak in intensity (Fay 1982). Timing birth to coincide with clement

conditions is clearly advantageous to the walrus neonate which has a relatively poorly developed insulation layer (Fay 1982). Although the endocrine mechanism by which implantation is triggered is unknown, there is evidence that some species use environmental cues such as photoperiod, nutrition or climate to help coordinate reproductive events (Harrison 1963; Follett 1984; Stewart *et al.* 1989; Boyd 1991).

The timing of implantation in the Atlantic walrus has yet to be determined accurately. The accuracy of the predicted date of implantation (x-intercept) from the inverse regression of fetal growth is dependent upon the size of the smallest actual measurements (Stewart *et al.* 1989). The smallest fetus measured in this collection (1.6 mm) was similar in size to newly implanted Pacific walrus embryos (Fay 1982) and can therefore be considered a good approximation of the blastocyst prior to nidation.

For the Pacific walrus, Fay (1982) reported unattached blastocysts in late May and newly implanted embryos in late June and early July, and estimated the modal date of implantation as 1 July. Mansfield (1958) subtracted an estimated gestation period of 380 days from the collection date of a full-term fetus (May 26) to arrive at a mean implantation date of May 11. An active gestation period of 380 days appears to be an over-estimate. Other investigators have shown that active gestation of the

walrus fetus takes approximately 11 months (Brooks 1954 cited in Fay et al. 1984; Fay 1982). Subtracting an 11-month gestation period from May 26 would suggest that implantation occurs in late June. Based on the inverse regression of fetal growth, implantation occurs approximately June 30th.

General Discussion

A suite of selective pressures act directly or indirectly to determine an organism's body size (Townsend and Calow 1981; Boyce 1988). Some of the selective advantages of large body size in mammals include: *i*) thermal advantages in cold climates (Mayr 1956; Reppening 1976); *ii*) the ability to store sufficient energy to survive periods of energetic deficiency (Pond 1981; Zeveloff and Boyce 1988); and *iii*) reduced risk of predation (Harvey and Read 1988).

As a marine mammal, walruses are pre-adapted to exist in an aquatic environment where thermal conductance is nearly 25 times that of air (Stahel and Nicol 1982). Large body size is by no means the only adaptive strategy to cold climates. Cold adaptations in mammals living in extreme environments usually include physiological adaptations such as increased insulation, as well as a variety of behavioral adaptations. In addition to being large-bodied, adult walruses are extremely well insulated by thick layers of subcutaneous fat (Mansfield 1958) and arctic air temperatures are mainly within the thermoneutral range for adult walruses (Fay and Ray 1968). Moreover, walruses are highly gregarious and will haul out in groups at any time of the year (Fay 1982). In cold weather, this huddling behavior offers a heat conserving advantage (Fay and Ray 1968). Also, during inclement conditions walruses tend to spend more time in the

water (Fay 1982), where the thermal environment remains constant at approximately -2°C (Dunbar 1977). The relatively large birth size of pinniped neonates may be adaptive to cold environments (Mayr 1956; Kovacs and Lavigne 1986; 1992). Walrus neonates are also darkly pigmented which may be adaptive to capturing the abundant solar radiation during the arctic spring.

The fasting endurance hypothesis predicts that in seasonal or unpredictable environments, selection will favor large body size and concomitantly large energy reserves because of higher survival during periods of energy deficit (Zeveloff and Boyce 1988). It has been noted that walruses exhibit considerable seasonal and individual variation in blubber stores, hence body mass (Fay 1982). Although seasonal feeding patterns in walruses are poorly understood, stomach content analyses indicate that feeding is reduced in July and August (Mansfield 1958; Fay 1982; Fisher 1989). This is consistent with Inuit reports that walruses are leanest during the summer months. The reason for reduced feeding during the summer months is unclear, but fasting appears to coincide with the annual moult (Fay 1982).

Periods of energy depletion also occur in connection with the reproductive cycle. Large body size in males may be promoted in part, through the ability to survive a prolonged fast during the breeding period (Stirling 1983; Riedman 1989). Sufficient energy reserves are crucial for adult males at this time as their

intake of food is minimal (Fay 1982). In females, large body size and energy reserves improve the ability to meet the energetic demands of fetal growth and lactation (Stewart and Lavigne 1984; Kovacs and Lavigne 1992).

In large mammals, predation tends to fall most heavily on juveniles (Van Valen 1973). Because of their large body size and formidable tusks, adult walruses have few natural predators. The principal natural predators of walruses; polar bears (*Ursus maritimus*) and killer whales (*Orcinus orca*), primarily target calves and yearlings (Fay 1982). Giving birth to large calves and extending the period of maternal care may be an adaptive strategy to reduce juvenile mortality.

The selective pressures promoting large body size are balanced in part by the energetic demands of maintenance and reproduction (Lavigne et al. 1982; Peters 1983). Increasing the allotment of resources for any one life function is done only at the expense of others (Boyce 1988). The price of large body size can be measured in part by reduced reproductive potential (Peters 1983). Since most physiological rates scale with body size, the duration of equivalent biological processes increase in larger animals (Townsend and Calow 1981; Lindstedt and Swain 1988). Consequently, large mammals tend to mature at an older age and have longer gestation periods and inter-birth intervals than smaller species (Eisenberg 1981). In compensation for reduced

reproductive potential, the life history of large mammals tends to be characterized by longevity and by low rates of natural mortality which act together to increase reproductive lifespan (Pianka 1978; Harvey and Zammuto 1985) and by extended periods of parental care which favors increased juvenile survivorship (Harvey and Read 1988).

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Comparative studies across different mammalian species have shown that the age of first reproduction is highly correlated with body size (Western 1979; Harvey and Zammuto 1985). Laws (1956) found that body-length at puberty was relatively constant across 12 species of pinnipeds, averaging 87% of final body length. He suggested that the age of sexual maturity is inversely proportional to the rate of growth. Larger species take longer to reach this threshold size and therefore mature at an older age (Laws 1956).

Walruses are large, slow growing pinnipeds, and sexual maturity is not achieved until several years after birth. The growth model for female walruses from Foxe Basin predicted that females achieve 87% of asymptotic body-length by the age of 9 years. Reproductive material from sub-asymptotic animals was insufficient to quantify the relationship between body size and sexual maturity, but the limited available data suggest that 9 years of age may be an overestimate of sexual maturity. One 6year-old specimen and all females 7 years of age or older had previously ovulated. The age of first reproduction is probably a better index of reproductive maturity in walruses. Primiparous specimens up to 12 years of age indicate that breeding maturity does not necessarily coincide with sexual maturity.

In mammals, the duration of gestation is highly correlated with maternal mass and with fetal size at birth (Martin and MacLarnon 1985; Harvey and Read 1988). Pinnipeds produce larger young than other mammals of comparable size and have a relatively longer gestation period (Laws 1959; Stewart 1983). The walrus neonate is large relative to other pinniped species and has the longest reported gestation period (Kovacs and Lavigne 1992).

In walruses, a 3-4 month period of embryonic diapause coupled with approximately 11 months of active gestation results in a supra-annual reproductive cycle. Long reproductive cycles are generally incompatible with highly seasonal environments which are characterized by short periods favorable for birth (Kiltie 1982, 1988). The degree of reproductive seasonality favored by natural selection depends upon the balance between lowered reproductive potential and the benefits of improved offspring survival. Since offspring survival is an important component of reproductive fitness, the costs of delayed reproduction associated with seasonal breeding may be offset by an extension of parental investment in previously produced offspring (Kiltie 1988).

The size of walrus calves at weaning is large relative to other pinniped species (Stewart 1983; Kovacs and Lavigne 1992). Unlike other ice-breeding pinnipeds which give birth to and wean their calves in one location (Stirling 1983) over a relatively short (2-6 week) period (Stewart 1983), walrus calves accompany their mother from birth and are not weaned until the age of 2-3 years (Mansfield 1958; Fay 1982; Miller and Boness 1983; Fisher 1989). The development of aquatic nursing appears to be central to this strategy. While most ice-breeding pinnipeds are dependant upon stored energy reserves to fuel their metabolic needs and meet the energetic demands of lactation (Stewart 1983), lactating female walruses are able to forage for food during the nursing period, allowing them to spread out the costs of lactation over an extended period (Kovacs and Lavigne 1992). The prolonged period of lactation allows walrus neonates to achieve an advanced developmental state during the period of energetic dependency on their mothers, which ultimately leaves them better equipped to forage and escape predators (Harvey and Read 1988; Kovacs and Lavigne 1992).

Life history characteristics can vary between temporally or geographically isolated populations of a species in relation to population density or food availability (Sergeant 1973; Pianka 1978). Resource-based models predict that as a population approaches its maximum population size or carrying capacity (K), competition for limited resources intensifies and selection will

promote later maturation and larger body size (MacArthur 1972; Pianka 1978). Because breeding animals must partition their metabolizable energy between maintenance and reproduction, the energetic costs associated with reproduction are proportionally greater in resource-poor environments. Pinnipeds have a large birth mass:maternal mass ratio (Stewart 1983), and maternal energetic investment is substantial (Stewart and Lavigne 1984). By delaying puberty, animals can achieve sufficient mass and life experience to maximize reproductive success (Boyd 1991).

In contrast, in an expanding population selection will favor maturation at an earlier age, because genotypes selecting for early reproduction are generated at a higher rate (bet-hedging and r-selection theories) (Stearns 1980; Pianka 1978; Townsend and Calow 1981). The selective advantages of producing offspring at an earlier age than breeding competitors are balanced by the costs of early reproduction which can be measured in terms of increased mortality rates and reduced subsequent reproductive success (May and Rubenstein 1984). For harp seals (Phoca groenlandica), Stewart (1986) found that fetal growth and lactation represented a fixed energetic cost independent of maternal age or size and that cost of reproduction was proportionally greater in smaller (younger) females, which had to devote proportionally more of their energy stores to successfully wean a pup. Early reproduction can also result in smaller final body size; female beaver (Castor canadensis) which experience an

early reproduction are small in body size and have reduced adult survivorship (Boyce 1981).

In other pinnipeds, shifts in population density have been linked to changes in maturation and fertility rates. Between 1950 and 1971 the population of northwest Atlantic harp seals declined by more than 50 % as a result of intense commercial harvesting (Winters 1978). During this time, the mean age of sexual maturity dropped from 6.2 to 4.5 years while pregnancy rates increased from 87 to 94 % (Bowen *et al.* 1981). These shifts in life history characters are likely mediated by differences in food availability along an r-K continuum (Pianka 1978; Innes *et al.* 1981; Stewart and Lavigne 1984).

In comparing the life history traits of Foxe Basin walruses with data collected from other populations of walruses, several lines of evidence support the hypothesis that the Foxe Basin stock is resource-limited. The similarity of growth parameter estimates generated for Foxe Basin walruses separated in time by more than 30 years may indicate that the population has remained relatively stable through this time, or alternatively, returned to a similar size. Comparisons of growth equations indicated that Foxe Basin walruses were significantly larger and reached full physical maturity at an older age than walruses collected from Hudson Bay in the 1950's. Mansfield (1958) postulated that the northern Foxe Basin population and Hudson Bay group

represented two separate stocks. During the late 1800's and early 1900's exploitation by whalers and commercial walrus hunters led to a significant decline in walrus stocks in Hudson Bay (Reeves 1978). Hudson Bay walruses examined in the 1950's are therefore likely to have been sampled from a depleted population of animals where selection may have favored early maturation over large final body size. Unfortunately, no marking or genetic data are available to validate the discrimination of these putative stocks, and a lack of recent Hudson Bay samples precludes comparisons of growth and maturation rates between the two contemporary groups.

Although the Pacific walrus has been considered the larger of the two subspecies (Mansfield 1958; Fay 1982), comparisons of growth equations indicated that Foxe Basin walruses were as long, or in the case of females, significantly longer than Alaskan walruses sampled in the 1970's. McLaren (1993) noted that the Alaskan animals were sampled during a period of rapid stock recovery where selection may have favored early maturity. Again, the size difference may indicate that the Foxe Basin walrus stock is closer to K than the Alaskan population was during the 1970's.

The reproductive rates of Foxe Basin females sampled for this study are somewhat lower than values reported for Pacific walruses sampled during the 1970's (Fay 1982). In Foxe Basin, the availability of food resources to nursing females may be near

the minimum level required to meet the energetic demands of lactation. If the energetic costs of lactation leave the mother in a depleted physiological condition, it may be energetically advantageous to delay reproduction until sufficient energy reserves can be built up to ensure reproductive success (Stewart and Lavigne 1984; Stewart 1986). Furthermore, the foraging capability of nursing walruses bestows greater flexibility in the duration of lactation and may serve as a buffer against variability in the availability of food resources (Kovacs and Lavigne 1992). If a calf has difficulty procuring sufficient food resources on its own, longer nursing periods and consequently longer inter-birth intervals could result. An assessment of the condition of nursing females and more specific data on the age and size of walrus calves at weaning are required to test this hypothesis.

The predictive equation relating standard length to body mass for Foxe Basin walruses produced significantly lower estimates of body mass than the isomorphic equation generated for walruses from Greenland. Although the comparison may be confounded by seasonal variation in body mass, the possibility that these differences reflect true allometric differences between the stocks cannot be ruled out. Greenlandic walrus stocks were significantly reduced by commercial hunting in the early 1900's and continue to sustain a significant native harvest (Reeves 1978; Born 1990). Considering the large pre-exploitation

populations once supported in Greenland, the existing depleted stocks are unlikely to be facing food shortages. In comparison, the relatively lean condition of Foxe Basin walruses may indicate lower nutritional status. Information on the seasonal foraging patterns of the respective stocks and indices of condition are required to rigorously test this hypothesis.

The hypothesis that the Foxe Basin walrus stock is resourcelimited must be interpreted cautiously. While large body size and delayed maturation may be characteristic of a stable population near carrying capacity, these traits may also reflect changes in the availability of food resources in response to environmental fluctuations or human disturbances (Innes et al. 1981). The latter hypothesis is more plausible for the Foxe Basin stock, which continues to support an annual subsistence harvest of approximately 215 walruses (Anderson and Garlich-Miller 1994). Indeed, the disappearance of large herds along the east coast of the Melville Peninsula has been attributed to increased boat traffic and hunting around the communities (Brody 1976). The abandonment of part of the traditional walrus range could result in an increase in population density in the remaining habitat. Furthermore, the remaining habitat may be characterized by less suitable foraging grounds than the traditional areas abandoned.

To summarize, the life history of the Atlantic walrus is characterized by large body size, late maturation, a supra-annual reproductive cycle and long inter-birth intervals. The inability to produce offspring in consecutive breeding cycles may, in part, be offset by extended parental investment in previously produced offspring to reduce juvenile mortality.

The productivity and survivorship of a species constrain the level of exploitation that a population can sustain and its ability to recover from depredation (Eberhardt and Siniff 1977; Taylor and DeMaster 1993). The results of this study indicate that the Atlantic walrus has an intrinsically low rate of natural increase. Historical evidence suggests that the range and abundance of the Atlantic walrus were significantly reduced by intensive commercial exploitation in the nineteenth and twentieth centuries (Reeves 1978). The commercial harvest of walrus by non-natives has been prohibited in Canada since 1928, however, existing stocks have shown little evidence of recovery (Reeves 1978; Richard and Campbell 1988).

Although the present status of walrus populations in the Canadian arctic is poorly known, northern Foxe Basin is believed to support one of the largest remaining concentrations of Atlantic walruses in the world (Reeves 1978; Richard and Campbell 1988). This stock of walruses continues to be a resource of considerable importance to the Inuit communities of Foxe Basin

(Orr et al. 1986; Anderson and Garlich-Miller 1994). In light of increasing economic development and human activity throughout the Arctic, careful management of existing walrus stocks is warranted. Part of this strategy should include continued research of walrus life history parameters from which sagacious conservation plans can be built.

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