VARIATION IN GROWTH AND SEASONAL CONDITION OF RINGED SEAL, PHOCA HISPIDA, FROM THE CANADIAN ARCTIC

BY

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A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

Department of Zoology University of Manitoba Winnipeg, MB

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

of

Doctor of Philosophy

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Abstract

Ringed seal (*Phoca hispida*) morphometric data from three locations in the eastern Canadian Arctic were compared to examine geographic variation in aspects of growth, life-history, and condition. Seals from Eureka (80° N) reached an asymptotic length of 150.9 cm, 14.0 cm greater than individuals from Arctic Bay (73° N) and 22.7 cm greater than those from Pangnirtung (66° N). Seals may reach sexual maturity sooner in Arctic Bay than Eureka or Pangnirtung. Statistically significant sexual dimorphism was evident in Pangnirtung where males were 6.7% longer than females. Condition, expressed as blubber content (% of total mass) was estimated using three published indices of condition: blubber thickness, axillary girth/length • 100, and the 'LMD' index. These indices did not adequately describe changes in condition for this data and did not provide a meaningful measure of the absolute amount of fat present. A new method of estimating absolute sculp (skin and blubber) mass from sculp volume calculated by a prolate spheroid model was developed. Regressions of mass in relation to length for various seasons demonstrated that spring and summer mass loss averaged 14 kg for an adult seal with an asymptotic length of 128 cm. Prior to sexual maturity, juveniles lost proportionally less mass than adults. Observed differences in growth and condition may reflect variation in life-history strategies related to primary productivity and predation pressure by polar bear (Ursus maritimus) and Inuit.

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Dedication
To all the friends and family who were there for me when I wasn't as strong as I
thought I should have been.
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CHAPTER ONE: GENERAL INTRODUCTION

Research Needs

The hypothesis that ringed seal (*Phoca hispida*) from the Canadian Arctic exhibit a clinal south-north increase in adult length has been noted several times in studies of their growth and general ecology (Soper 1944; McLaren 1958, 1993; Smith 1973).

The first comprehensive study of ringed seal in the eastern Canadian Arctic was conducted by McLaren (1958). He compared the adult length of individuals from southwestern Baffin Island north to Ellesmere Island using growth curves fitted by eye and lines of linear least squares. No statistical comparisons of the growth curves were performed but it was observed that adult length increased with latitude. These differences were attributed to the stability of the ice substrate upon which pups were whelped. He postulated that individuals reared on complex coastlines with stable and persistent ice cover would have longer lactation periods and show better growth than ringed seals from simple coastlines with unstable, shifting ice cover. He also suggested that the increased duration of ice cover at higher latitudes would also favour enhanced pup growth. Thus, increase in size was the result of both the stability of the breeding habitat and the duration of ice cover as a function of latitude. Other researchers have evoked similar reasoning to propose the existence of two

distinct ecotypes of the ringed seal; one comprising large individuals inhabiting the stable fast ice and another of smaller individuals occupying areas of shifting pack ice (Fedoseev 1975; Finley et al. 1983).

Smith's (1973) monograph focused on the population dynamics of ringed seal in the Cumberland Sound and Home Bay regions of southeastern Baffin Island. He found statistically significant differences (*t*-tests) between the adult size of seals from Home Bay, Hoare Bay, and Cumberland Sound, with those from Home Bay being the longest. Mean adult lengths varied from 120 to 130 cm, Hoare Bay individuals being 9.10% longer than those in Cumberland Sound. Due to the instability of Cumberland Sound ice and relative stability of Home and Hoare Bay, this difference in length was attributed to McLaren's 'stability of the ice substrate' hypothesis. Smith (1987) later documented the ecology of ringed seal in the Victoria and Banks Island regions of the western Arctic. Adult males in this region were estimated to have an asymptotic length of 131 cm while females attained 127 cm. Females attained 86.3% of their asymptotic length by first reproduction at 7.67 years while males achieved 89.6% of their asymptotic length by sexual maturity (approx. 7 years).

McLaren (1993) conducted a substantial review of pinniped growth in which he further examined geographic variation in the asymptotic length of ringed seal. Substantial variation was found throughout their circumpolar range and most was attributed to his earlier 'stability of the ice substrate hypothesis'. He did note, however, that data from the Baltic Sea and Svalbard were not compatible

with this hypothesis. Although some comparisons between locations were tested using likelihood ratio tests, no formal results were reported for his data from Baffin Island.

Annual variation in the condition of ringed seal has only been studied incidentally (McLaren and Smith 1985). The major monographs concerning ringed seal biology in the Canadian arctic (i.e. McLaren 1958; Smith 1973, 1987) have all dealt with the subject to varying degrees. Methods of estimating condition vary from simple (girth/length) • 100 and blubber depth indices to more complex empirical estimators such as (length/mass)^{1/2} • blubber depth (Ryg et al. 1990). Many of these indices, especially the girth/length ratio, have been regarded as insensitive, failing to discriminate animals in states of obvious starvation (McLaren and Smith 1985) and none accurately estimate the absolute amount of fat a seal contains.

Examination of this literature revealed several research needs:

 The need to statistically validate the observation that ringed seal adult length is greater in the high Arctic and N. Baffin Island than in S. Baffin Island.

- The need to better understand patterns of ringed seal growth to determine whether other aspects of growth also varied among locations.
- 3. The need to assess seasonal condition in ringed seal so that future research may integrate both aspects of growth and condition with the ultimate goal of monitoring the status of ringed seal populations that are nutritionally, culturally, and economically important to Inuit.

Thesis Background and Objectives

The morphometric data presented in this thesis were collected by Inuit or scientific researchers as part of an ongoing project conducted by the Department of Fisheries and Oceans concerning the reproductive biology of ringed seal. It includes data collected from Eureka on Ellesmere Island in 1994, from Arctic Bay on N. Baffin Island in 1993, and from Pangnirtung on S. Baffin Island between 1990-1996.

The main goals of this thesis are:

1. Statistically compare three samples of ringed seal collected from 66° N to 80°N in the Canadian Arctic to test the hypothesis that individuals at

higher latitudes achieve a longer adult length than those from more southerly regions.

- Examine morphometric data taken from ringed seal in Pangnirtung, NU
 between 1990 and 1996 to explore patterns of condition and develop
 new ways of estimating seasonal fluctuations in mass.
- 3. Report other related aspects of ringed seal growth such as length at birtin, absolute rate of growth at birth, and age-specific rates of growth.

The knowledge gained from this study will lay the foundation for future analysis, exposing potential research questions and, as the information base grows in the coming years, will permit the evaluation of new methods of describing growth and condition.

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CHAPTER TWO: VARIATION IN GROWTH OF RINGED SEAL (PHOCA HISPIDA) FROM THE EASTERN AND HIGH CANADIAN ARCTIC

Abstract

Ringed seal (Phoca hispida) morphometric data from three locations of increasing latitude in the eastern Canadian Arctic were compared to examine geographic variation in aspects of growth and life history. Growth in length was best described using a three-parameter logistic model. Seals from Eureka (80° N) reached an asymptotic length of 150.9 cm, 14.0 cm greater than individuals from Arctic Bay (73° N) and 22.8 cm greater than those from Pangnirtung (66° N). Individuals achieved 95% of adult length by 6.8 years in Arctic Bay, 8.6 years in Pangnirtung, and 10.4 years in Eureka suggesting that ringed seals may reach sexual maturity sooner in Arctic Bay than the other two locations. Statistically significant sexual dimorphism was evident in Pangnirtung where males were 6.7% longer than females. No significant differences in growth parameters were found when the present results were compared to data collected from the same locations in the 1950's. Observed differences in growth may reflect variation in life history strategies related to primary productivity and predation pressure by polar bear (*Ursus maritimus*) and Inuit.

Introduction

The ringed seal, *Phoca hispida* (Schreber), is an abundant circumpolar marine mammal capable of inhabiting fast sea ice by maintaining breathing holes by scraping with its foreclaws (Smith and Stirling 1975). Pups are born from mid-March to mid-April in protective subnivean lairs constructed in snowdrifts overlying access holes (Smith and Stirling 1975; Furgal et al. 1996). Pups are approximately 65 cm in length at birth and are weaned after a 36-41 day lactation period, having reached a mean length of 88 cm and an average mass of 22.1 kg (McLaren 1958; Hammill et al. 1991). Adult length ranges from 1.2 to 1.5 m and body masses exceeding 90 kg are common (McLaren 1958). Ringed seal is the primary food of polar bears (*Ursus maritimus*) and is of great nutritional, cultural, and economic value to Inuit (Stirling and McEwan 1975; Kingsley 1990).

In a comprehensive review of pinniped growth, McLaren (1993) examined regional variation in adult body length of ringed seal throughout their circumpolar range. In the Canadian Arctic specifically, ringed seals from the northeastern and high Arctic were longer as adults than those from more southerly regions. No statistical tests of these differences were provided. McLaren concluded that the observed variation in length was due to the stability of the ice substrate on which pups were whelped. He postulated that in northern regions with stable and persistent ice cover, individuals might have longer lactation periods and show

better growth than ringed seals from more southerly areas with unstable and shifting ice cover. Other researchers have evoked similar reasoning to propose the existence of two distinct ecotypes of the ringed seal; one of large individuals inhabiting the stable fast ice and another of small individuals occupying shifting pack ice (Fedoseev 1975; Finley et al. 1983).

This paper examines ringed seal morphometric data collected between latitudes 65° and 80° N in the Canadian Arctic. The purpose is to further examine and statistically test the hypothesis that individuals of the high Arctic achieve a larger adult length than those from more southerly regions. Other aspects of growth such as estimated length at birth, age-specific rates of growth, and sexual dimorphism are also investigated.

Materials and Methods

Morphometric measurements were made on ringed seals killed by Inuit or researchers between August 1990 and July 1996 near Eureka on Ellesmere Island (80°00'N, 85°40'W), Arctic Bay on northern Baffin Island (73°05'N, 85°20'W), and Pangnirtung on southern Baffin Island (66°05'N, 65°45'W) (Figure 2.1). Animals were taken from leads or breathing holes during the winter and

Figure 2.1. Ringed seal sampling locations in the eastern and high Canadian Arctic.



spring hunting season and from the open water during the summer and fall hunting season. Standard length and axillary girth (American Society of Mammalogists 1967) were measured to the nearest centimeter and body mass, including gut contents was recorded to the nearest kilogram. Individuals from Arctic Bay and Pangnirtung were later aged by counting growth layer groups in the dentine of undecalcified, unstained thin cross-sections of canine teeth while samples collected from Eureka were aged by counting growth layer groups in the cementum of decalcified, stained longitudinal sections (Smith 1973; Stewart et al. 1996). This reason for this difference in method and its implications will be discussed later. Ages were expressed in days based on a nominal birth date of April 1 as in Stewart et al. (1998).

Various growth models were evaluated to determine that which best fit the data. These included three-parameter forms of the Gompertz, von Bertalanffy, and logistic as parameterized by Hammill et al. (1995):

[1] Gompertz
$$I_{t} = L_{-} \left(\frac{I_{o}}{L_{-}} \right)^{\exp \left[\frac{K_{o}t}{I_{o} \ln(I_{o}/L_{\infty})} \right]}$$

[2] von Bertalanffy
$$I_t = L_{-}\left(1 - \left(1 - \left(I_o / L_{-}\right)\right) \cdot \exp\left[\frac{-k_o t}{\left(L_{-} - I_o\right)}\right]\right)$$

[3] logistic
$$I_{t} = L_{\infty} / \left(1 + \left(L_{\infty} / I_{o} - 1 \right) \cdot exp \left[\frac{-k_{o}t}{I_{o} (1 - \left(I_{o} / L_{\infty} \right))} \right] \right)$$

where:

 l_t = length at time t

L. = asymptotic length (cm)

 l_0 = estimated length at birth (cm)

 k_0 = absolute rate of growth at birth (cm·year⁻¹)

A four-parameter von Bertalanffy model, as parameterized by McLaren (1993), and a two-parameter exponential model were also examined:

[4] von Bertalanffy
$$I_t = L_{-}(1-e^{a(t-t_o)})^b$$

[5] exponential
$$I_t = L_{\infty} (1-e^{-mt})$$

where:

 l_t = length at time t

L. = asymptotic length (cm)

a = rate of approach to asymptote

b = curvilinearity of approach to asymptote

 t_0 = start of embryonic growth

m = fitting constant

Growth models were fit to length-at-age data using the nonlinear (NLR) program of SPSSTM Ver. 6.1.3, specifying the sum of squared residuals loss function. NLR provides parameter estimates, an asymptotic standard error with 95% confidence intervals based on the *t*-distribution, and the asymptotic correlation matrix of parameter estimates. The most appropriate model was selected on the basis of Akaike's Information Criterion (AIC):

[6] 2 • (# of free parameters in the model) -2 • (maximum log likelihood of the model) (Akaike 1974)

where maximum log likelihood is calculated as:

[7]
$$\operatorname{Ln}(\operatorname{L}\{X \mid \mu, \sigma\}) = \operatorname{Ln}\left(\frac{1}{\sigma\sqrt{2\pi}}\right) - \frac{(X-\mu)^2}{2\sigma^2}$$

Other statistical considerations such as the standard errors of curve parameters and r² values were also considered.

The influence of any given measurement on the calculation of asymptotic length and AIC was determined by jackknifing each dataset and recalculating values with the remaining points (Efron 1979).

All comparisons of ringed seal growth curves, including the comparison of curves from the current study and those constructed from existing literature data, were carried out using likelihood ratio tests for unequal sample size and equal variance (Kimura 1980). All comparisons were made at a significance level of α = 0.05. Homogeneity of regression sample variance, an assumption in the comparison of two populations (sampling locations) under the likelihood ratio method (Kimura 1980), was determined using Bartlett's test (Snedecor and Cochran 1980).

To determine if the growth curves derived in the present study were representative, especially those for Eureka (n=18) and Arctic Bay (n=37), comparisons were made with published data (McLaren 1958). McLaren's morphometric data from Pangnirtung (n=113), N. Baffin Island (n=25) and Ellesmere Island (n=4) were added to the data collected in the present study from Pangnirtung, Arctic Bay and Eureka, respectively, to examine whether the curves were significantly altered.

Results

Samples

The sex ratios (F:M) of the samples ranged from 1:1 in Arctic Bay and Pangnirtung 1992/93 to 1:1.6 in Pangnirtung 1996. Only the Pangnirtung 1996 sample was significantly different from 1:1 ($\chi^2 = 4.85$, df = 1, p = 0.03). Females were outnumbered by males 1:1.3 when the Pangnirtung samples were pooled.

All samples, except that from Eureka, showed a bias towards young (newborn through 3 years) individuals. Seals collected from Pangnirtung in 1990/91 were almost exclusively from this age group (Table 2.1). The mean age of seals collected from Arctic Bay was 5.0 ± 5.7 years (\pm 1 SD) and was not significantly different from the mean age of 5.2 ± 4.6 years from Pangnirtung (1990-1996 pooled; p = 0.830). The mean age of those sampled in Eureka was 13 ± 12.2 years with two animals exceeding 30 years of age.

Mean length was greatest for seals collected from Eureka at 134.6 cm for females and 127.4 cm for males. Mean lengths were much shorter in the other samples with lengths ranging from 101.0 to 117.5 cm. Mean mass increased from 40.1 kg for females and 41.7 kg for males in Pangnirtung (1990-1996 pooled) to 82.4 kg for females and 73.5 kg for males in Eureka.

Table 2.1. Summary statistics for samples used in data analysis (means, ±1SD unless otherwise noted).

Datasets	Sex	N	Mean Age (yr + range)	Mean Length (cm)	Mean Weight (kg)	Mean Axillary Girth (cm)
Eureka 94	F	10	17.5 (0.2-38.2)	134.6 ±23.8	82.4 ±33.8	105.8 ±17.2
	M	8	7.4 (0.2-21.2)	127.4 ±12.5	73.5 ±37.1	103.1 ±18.5
Arctic Bay 93	F	19	3.3 (0.04-15.2)	101.0 ±24.7	38.4 ±28.0	84.6 ±25.4
•	M	18	6.8 (0.06-21.1)	117.5 ±23.8	59.3 ±30.1	99.9 ±19.6
Pangnirtung 90/91	F	30	2.6 (0.5-7.8)	100.5 ±11.7	35.4 ±11.6	87.0 ±8.2
r angimitang coro i	M	42	3.6 (0.4-10.5)	104.6 ±14.3	40.4 ±16.1	88.4 ±12.7
Pangnirtung 92/93	F	67	5.5 (0.2-14.6)	111.8 ±11.8	42.4 ±13.2	91.5 ±12.0
·g	M	68	4.8 (0.5-16.3)	111.0 ±12.7	41.9 ±14.0	90.1 ±11.8
Pangnirtung 96	F	35	5.9 (0.3-21.8)	110.1 ±11.4	39.7 ±12.1	84.9 ±13.4
i dilgimitalig oo	М	56	7.3 (0.3-38.2)	112.6 ±14.2	42.5 ±15.3	87.4 ±14.2
Pangnirtung Pooled	F	132	4.9 (0.2-21.8)	108.8 ±12.4	40.1 ±12.8	88.8 ±11.9
g.m.ang i oolod	M	166	5.3 (0.3-38.2)	110.0 ±13.9	41.7 ±14.9	88.7 ±12.9

Axillary girth was also greatest in the Eureka sample at 105.8 and 103.1 cm for females and males, respectively. There was little difference in axillary girth between the other samples or between the sexes at any site.

Growth

Fitting of the logistic three-parameter growth model resulted in the smallest AIC estimate for the Eureka 1994, Pangnirtung 1990/91, Pangnirtung 1992/93, and Pangnirtung Pooled samples (Table 2.2). The three-parameter von Bertalanffy model provided the best fit for the Pangnirtung 1996 sample and the four-parameter von Bertalanffy model provided the best fit for the Arctic Bay 1993 sample. The two-parameter exponential model had the highest AIC values in all cases. In addition to having the smallest AIC values, parameter estimates of the three-parameter logistic model had lower standard error values, were not as highly correlated with each other as the other models evaluated, and resulted in growth curves with slightly higher r² values. AIC values derived from jackknifing the datasets always showed the same rank ordering for each model tested as the original datasets. For Eureka 1994, Pangnirtung 1990/91, 1992/93, and 1990-1996 pooled this order was Logistic < Gompertz < von Bertalanffy. Based upon this information, the logistic model was chosen for further between- and among-

Table 2.2. Akaike's Information Criteria for two-parameter model (exponential), three-parameter models (Gompertz, von Bertalanffy, and logistic), and four-parameter model (von Bertalanffy) nonlinear functions. Bold type denotes the minimum AIC estimate for each dataset.

	2 Parameters		4 Parameters ²		
Datasets	Exponential	Von Bertalanffy Gompertz Logistic			Von Bertalanffy
Eureka 94	152.60	129.23	129.73	128.80	133.15
Arctic Bay 93	312.90	281.66	281.42	281.92	280.63
Pangnirtung 90/91	554.96	502.28	502.37	502.21	· 503.96 ·
Pangnirtung 92/93	1054.95	937.66	937.93	937.43	941.39
Pangnirtung 96	725.73	640.04	639.95	640.20	641.33
Pangnirtung Pooled	2353.50	2073.71	2073.92	2073.67	2080.40

¹Hammill et al. 1995

²McLaren 1993

group testing. Samples from Pangnirtung had similar regression sample variances ranging from 7.49 - 7.80, while Eureka and Arctic Bay showed variances of 6.93 and 9.80 respectively. However, the Bartlett's test indicated no significant differences in regression sample variance among any of the locations (p = 0.1).

Inter-annual Comparisons of Growth (Pangnirtung)

Multi-year data from the same location was available only for Pangnirtung. Among the 1990/91, 1992/93, and 1996 samples, asymptotic length ranged from 127.4 cm in 1990/91 to 128.9 cm in 1992/93. Absolute rate of growth at birth ranged from 6.03 cm·yr⁻¹ in 1992/93 to 7.72 cm·yr⁻¹ in 1990/91, and length at birth ranged from 85.3 cm in 1990/91 to 91.6 cm in 1992/93. No significant differences in any growth parameter among the Pangnirtung 1990/91, 1992/93, or 1996 samples were observed with the exception of a statistically significant difference (p = 0.045) in length at birth between Pangnirtung 1990/91 and 1992/93.

Sex-specific Comparisons of Growth (All sites, all years)

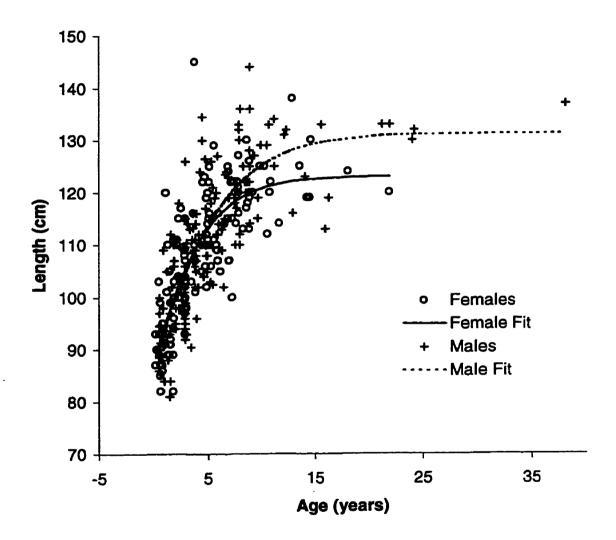
Significant sexual dimorphism was observed in the Pangnirtung 1996 sample with males being 131.1 cm long, 11.3% (13.3 cm) longer than females at 117.8 cm long (p = 0.038). When the Pangnirtung samples were pooled (1990-1996), males had an estimated asymptotic length of 131.3 cm, approximately 6.7% (8.2 cm) longer than that of females which achieved 123.1 cm in length (Figure 2.2). This dimorphism was also significant (p = 0.027).

Male and female curves diverge at about 5 years of age when female growth levels off. Males continued to grow for several more years. While females had achieved 95% (116.9 cm) of their asymptotic length by 6.7 years of age, males did not reach 95% (124.7 cm) of theirs until 9.7 years. Such differences were not evident among the other groups when examined individually or when the Eureka and Arctic Bay samples were combined in an effort to increase sample size. For all samples separated by sex, the remaining growth parameters, l_0 and k_0 , were non-significant.

Regional Comparisons of Growth (Eureka, Arctic Bay, Pangnirtung)

As there were no statistically significant differences in growth parameters among years at Pangnirtung (except length at birth 1990/91 vs. 1992/93), all

Figure 2.2. Logistic growth curves of male and female ringed seals collected from Pangnirtung (1990-1996).



regional comparisons were made based on a Pangnirtung 1990-1996 pooled sample. As sex-specific differences were found only in Pangnirtung and separating for the other sites would reduce sample sizes beyond practical value, the sexes were also combined.

Growth curve r² values were high for the Eureka (0.91) and Arctic Bay (0.85) samples but comparatively low for Pangnirtung (0.66). Individuals from Eureka had an asymptotic length (L_w) of 150.9 cm, 14.0 cm greater than those from Arctic Bay (L_w = 136.9 cm) and 22.8 cm greater than those from Pangnirtung (L_w = 128.1 cm, Table 2.3). Estimated length at birth (I₀) ranged from 94.5 cm in Eureka to 80.7 cm in Arctic Bay with Pangnirtung falling in between at 88.0 cm. Absolute rate of growth at birth (k₀) in Pangnirtung was 6.86 cm·yr⁻¹, slightly less than Eureka's 8.24 cm·yr⁻¹ and almost half that of Arctic Bay at 12.54 cm·yr⁻¹.

Asymptotic length was significantly different in all cases, as was estimated length at birth except for between Eureka and Pangnirtung (p = 0.114) (Table 2.4). Absolute rate of growth at birth differed substantially between Arctic Bay and Pangnirtung (p < 0.001). Jackknifing the samples revealed that no single data point was responsible for more than a 2.0% ($2.6-3.0 \, \text{cm}$) change in asymptotic length for any site, even in the very small Eureka sample. Percentage change per individual in the larger Arctic Bay and all Pangnirtung samples was negligible (< 1.0 cm). Changes in asymptotic length were generally

Table 2.3. Parameter estimates (SE), R² values, and 95% asymptotic confidence intervals for the logistic growth function. L_m=asymptotic length (cm), k₀=absolute growth rate at birth (cm·year⁻¹), and l₀=length at birth (cm).

Dataset	L.,	K₀	ما	R ²	95% Asymptotic Cl
Eureka 94	150.9 (3.05)	8.24 (1.80)	94.48 (3.79)	0.91	144.4 – 157.4
Arctic Bay 93	136.9 (3.94)	12.54 (2.30)	80.68 (2.79)	0.85	128.9 ~ 144.9
Pangnirtung 90/91	127.4 (6.85)	7.72 (1.77)	85.33 (2.36)	0.68	113.7 – 141.1
Pangnirtung 92/93	128.9 (3.40)	6.03 (1.12)	91.59 (2.18)	0.62	122.2 – 135.7
Pangnirtung 96	128.3 (2.60)	6.78 (1.15)	86.53 (2.87)	0.65	123.1 – 133.5
Pangnirtung Pooled	128.1 (1.85)	6.86 (0.68)	88.03 (1.33)	0.66	124.5 – 131.8

Table 2.4. Comparisons of growth curve parameters between Eureka, Arctic Bay, and Pangnirtung. * p< 0.05, ** p< 0.01, NS p > 0.05.

Datasets	Eureka 94	Arctic Bay 93	Pangnirtung Pooled
Eureka 94	•	•	-
Arctic Bay 93	L. **, ko NS, lo **	-	-
Pangnirtung Pooled	L., **, ko NS, lo NS	L., *, k ₀ **, l ₀ *	-

greatest with the removal of data points near the approach to the asymptote. Removal of lengths-at-ages beyond the 10 year mark had little effect on asymptote value. The addition of McLaren's data from the 1950's did not significantly alter the parameters of any of the curves derived in the present study.

A graphic comparison of logistic growth curves (Figure 2.3) illustrates differences in asymptotic length among the three sampling locations. Also, ringed seals caught in Arctic Bay have a more rapid growth rate than samples from either Pangnirtung or Eureka, achieving 95% of asymptotic length by 6.8 years of age. Seals from Pangnirtung reach 95% of their asymptotic length by 8.6 years of age and this value increases to 10.4 years for Eureka (Figure 2.4). This holds when animals less than 1 year of age are excluded from the graph removing the possibility that an incorrectly estimated length at birth causes this difference.

Figure 2.3. Logistic growth curves of ringed seals collected from Eureka, Arctic Bay, and Pangnirtung (1990-1996). Data for males and females are pooled.

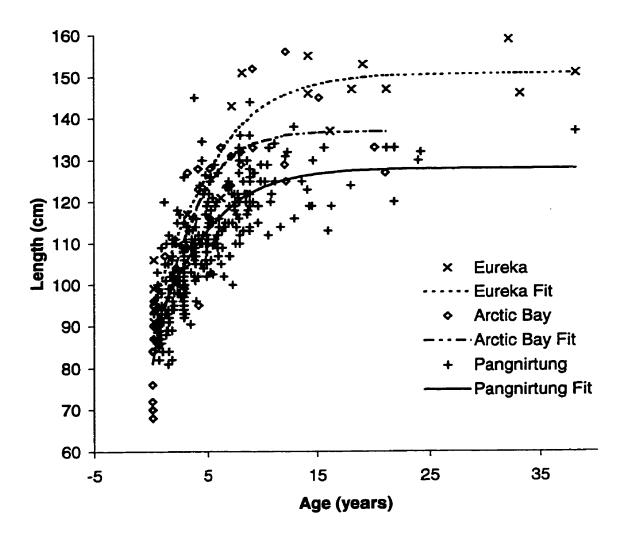
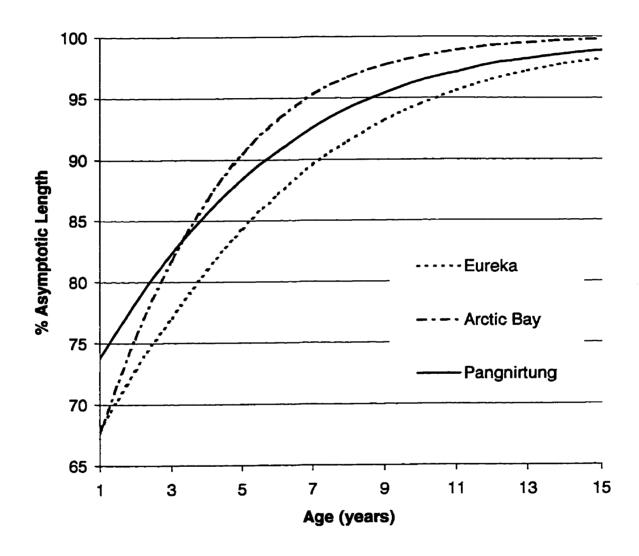


Figure 2.4. Age-specific growth rates (% of asymptotic length) for ringed seals collected from Eureka, Arctic Bay, and Pangnirtung (1990-1996). Growth during the first year is excluded from the graph.



Discussion

Ageing

The growth curves in this study were estimated from cross-sectional data and represent the 'average' growth of individuals born within each population over almost four decades. An accurate picture of growth requires that samples include adequate numbers of individuals and be representative of both sexes and all major age classes over a discrete period, i.e. from one breeding season to the next. Potential biases affecting the accuracy of growth curves include bias in the ageing method (see Stewart et al. 1996), incorrect ageing of individuals, over-representation of young or easy-to-capture individuals, and variation in birth dates when ages are assigned higher precision by backdating to a single date (April 1 in this study). Of these biases, incorrect ageing is potentially the most damaging (Leberg et al. 1989) and the implications of such errors in the present study were examined in some detail.

There is no series of known-age specimens for the ringed seal.

Traditionally, individuals have been aged by counting growth layer groups

(GLGs) in the dentine of unstained cross-sections of canine teeth (McLaren 1958; Smith 1973). Stewart et al. (1996) recently compared this method to

counting GLGs in the cementum of decalcified and stained longitudinal sections of canine teeth. The latter technique was determined to be the better method of ageing, especially for individuals ≥ 10 years of age where GLG counts of dentine and cementum differ the most. In the present study, animals collected from Eureka were aged by counting GLGs in the cementum, while the Arctic Bay and Pangnirtung samples were aged by counting GLGs in the dentine. This did not pose a significant concern with respect to parameter estimates. Jackknifing the samples showed that the asymptote (L.,) was defined by individuals aged between 5 and 9 years located on the approach to the asymptote and not by individuals that were aged greater than 10 years. When 20% of the individuals younger than 10 years of age from Pangnirtung were randomly adjusted by +/- 1 to 2 years to simulate errors in ageing, the asymptote of the resulting growth curve was never changed by more than 1.0 cm. Thus, the growth equations for ringed seals are robust to errors in ageing of individuals as determined from growth layer counts in dentine. This complements the observations of Leberg et al. (1989) that the asymptote itself is robust to errors in age estimation. Also, individuals older than 10 years were few in most samples (except Eureka) and did not contribute greatly to the shape of the resulting growth curve.

Quantitative Appropriateness of Growth Models

For length-at-age growth curves, especially those that do not exhibit a distinct inflection point, several growth functions fit the data well (Hammill et al. 1995). Further, every dataset-model combination will vary slightly in statistical properties (Ratkowsky 1983) and in some cases the choice of model will depend on the specific biological question being asked. For these reasons, it is essential that any model applied to growth data be examined for both goodness of fit and biological appropriateness.

In nonlinear regression, r² estimates of multiple correlation are not entirely suitable for assessing the goodness of fit of different models (Ratkowsky 1983). Akaike's Information Criterion (AIC) provides a simple, objective means of choosing among competing models by selecting the model that displays the minimum AIC estimate (MAICE). AIC uses maximum likelihood estimation to determine those values of the parameters for which the observed data are most likely. A penalty for each parameter added to the model is incorporated in the AIC. This approach, which promotes parsimony in parameter number, is desirable because in general, as more parameters are added to a model, the ability of the data to actually estimate all of the parameters diminishes (Ratkowsky 1983). Also, correlation among these parameters may increase making it difficult to interpret the particular effects of individual parameters (Hilborn and Walters 1992). In this study, differences among AIC values for a

particular dataset are small, however, jackknifing showed that these differences were consistent. In addition, the AIC also selected the model which displayed the lowest parameter standard errors and the highest estimates of r^2 . A high r^2 value does not necessarily mean a given model is appropriate. The agreement between AIC and r^2 values is due to the fact that the various models tested all had 3 or 4 parameters. In theory, as one increases the number of parameters, the r^2 value would also increase until the number of parameters equaled the number of data points and $r^2 = 1.0$. However, the penalty assigned by the AIC after even a small number of parameters were added to the model would be great and a simpler model would be favoured (Akaike 1974).

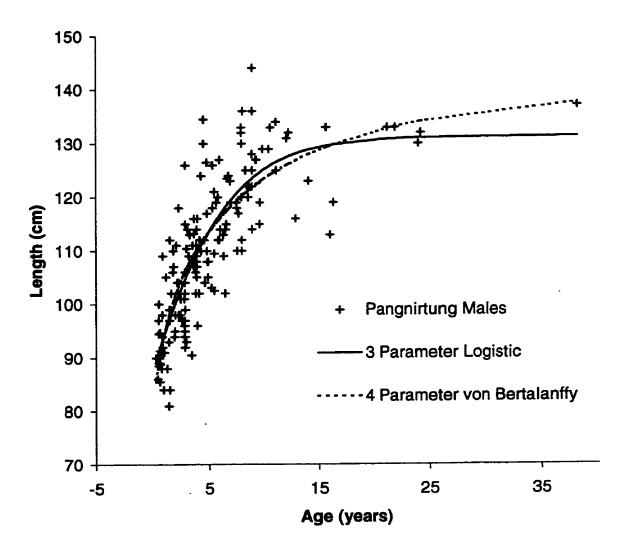
Biological Appropriateness of Growth Models

The general 4-parameter von Bertalanffy growth function has been promoted as an appropriate model for pinniped growth and a good standard for comparing future growth data (McLaren and Smith 1985). The data in the present study, however, indicate that the 4-parameter model may not provide the best description of ringed seal growth, especially for estimating the asymptote.

As used by McLaren (1993), the 4-parameter von Bertalanffy model was actually a three-parameter model. McLaren anchored the age-at-zero-length

(blastocyst implantation) parameter to an a priori value (-0.61 years) based on embryonic growth data and a birth date in early April. Possible regional variation of aspects of ringed seal life history such as fetal growth and birth dates are not well understood and constraining any aspect of a model should be avoided. McLaren also excluded all individuals less than one year of age because of rapid growth during that period. This exclusion results in the biasing of the shape of the growth curves towards older age classes (Garlich-Miller and Stewart 1998). For fitting purposes, length at birth was assumed to be 65 cm. This estimate of length at birth was based on 3 full-term fetuses and 2 newborns collected from the eastern Canadian Arctic (localities unstated). In the Arctic Bay sample of the present study, the mean length of pups with umbilical cords present was similar at 69.5 cm (n=4, SD=1.0). However, smaller pups have been observed including a newborn from Strathcona Sound, north Baffin Island in 1997 measuring 48 cm (M. Goodyear and S. Innes, unpublished data). Finally, when used in this parameterization, the von Bertalanffy function tends to overestimate asymptotic length unless one assumes that growth in body length continues throughout life (Figure 2.5). Owing to the small sample sizes in the older age classes, the cross-sectional nature of the data, and well-established patterns of basic mammalian development there is no reason to suggest growth is indeterminate.

Figure 2.5. A comparison of the four-parameter von Bertalanffy growth model (McLaren 1993) and the three-parameter logistic growth model (Hammill et al. 1995).



The three parameter logistic model, as parameterized in Hammill et al. (1995), in addition to showing the minimum AIC estimate, has several advantages over McLaren's four parameter model: all age classes may be included in the analyses allowing the available data to define early growth; no assumptions are made regarding when embryonic growth commences; and parameters are defined in biologically meaningful terms such as asymptotic length, length at birth and absolute rate of growth at birth. Datasets that exhibit a well defined asymptote, i.e. growth is truly asymptotic, also converge readily.

The Hammill et al. (1995) model does have several drawbacks that may be significant depending on the nature of the research question being asked. Differences in length at birth (I₀) in this study were unreliable as the value of this parameter relies heavily on obtaining a reasonable sample of newborn individuals. As mentioned earlier, newborn ringed seals were present in only the Arctic Bay sample. For this reason, length at birth in Eureka and Pangnirtung may have been overestimated. The absolute rate of growth at birth (K₀) is a specific 'point-in-time' estimate and reveals little about overall pup growth and is also affected by the under-representation of newborns. Research focusing on early development in pinnipeds is usually studied with large samples of very young animals using simple linear regression (Stewart and Lavigne 1984; Kovacs and Lavigne 1986). Growth after one year is well described by the 3-parameter logistic curve despite some overestimation of length at birth. Of all

parameters, asymptotic length is the most robust and is only slightly affected by incorrect ageing of the older age classes. In light of these biological justifications, as well as statistical reasons discussed earlier, the three-parameter logistic growth model as parameterized by Hammill et al. (1995) suitably describes growth in ringed seals for the data examined in this paper.

Inter-annual Comparisons of Growth

Except for length at birth between 1990/91 and 1992/93, there were no significant differences in any parameter between years for Pangnirtung. The apparent inter-annual stability of growth parameters supports the argument that the growth curves for Eureka and Arctic Bay can be assumed to be representative of their populations and not the result of annual variation in growth. This conclusion is further strengthened by comparison with past data from Eureka, Arctic Bay, and Pangnirtung collected in the 1950's by McLaren (1958). Addition of this past data did not significantly change the parameters of the curves. The annual stability of growth parameters in Pangnirtung implies that growth varies little year to year in response to environmental conditions or food resources. An examination of cohorts extracted from the 1990-1996 cross-sectional data did not contradict this view.

Sex-specific Comparisons of Growth

Male ringed seals from Pangnirtung (1990-1996 pooled) achieved an asymptotic length approximately 8 cm longer than females. No difference was observed in any of the other growth parameters suggesting that growth between the sexes may only differ with respect to final adult body length. Divergence of the two curves becomes apparent at 5 years, a point by which 20 to 60 percent of females in this region were found to be sexually mature (Smith 1973). By comparison, most males are sexually mature at about 7 years (Smith 1973). Laws (1956) found that for most female pinnipeds 86% of asymptotic length was achieved by sexual maturity. This does not fit well with the present data which places 86% of growth complete by 3 years. Smith (1973) did not find any evidence of ovulation among 134 ovaries from individuals of up to three years of age collected from the Pangnirtung region. Reproductive tracts obtained from seals in the present study are currently being analyzed. As there was no difference in asymptotic length between the sexes when each subsample from Pangnirtung was analyzed individually, sample sizes in excess of at least 100 individuals are probably needed to reveal sexual dimorphism. This would be similar to the situation in harp seals where slight sexual dimorphism was not demonstrated until sample sizes in the literature became sufficiently large in the early 1990's (Innes et al. 1981; Hammill et al. 1995).

Regional Comparisons of Growth

Among the three locations studied in this paper, growth varied with respect to adult body size (L.,) and pattern of growth. Differences in body size are reflected in the increase in asymptotic length with increasing latitude while differences in the pattern of growth are a result of the rate at which adult size is achieved. Although McLaren (1993) showed regional differences in size among pinnipeds with large ranges, i.e. harbour and grey seals, such strong clinal increases in asymptotic length were not noted for species other than the ringed seal.

The observed increase in asymptotic length with increasing latitude was statistically significant. These results were consistent with Bergmann's rule (Bergmann 1847) which states that body size within a species increases with latitude due to a resulting decrease in the ambient environmental temperature. This hypothesis remains controversial due to disagreement on the interpretation and intent of the original text (see Geist 1987, 1990; Paterson 1990), a large body of literature detailing numerous exceptions to the rule (McNab 1971), and equivocal attempts to develop physiological arguments in support of the rule (Searcy 1980; Steudel et al. 1994). In most cases today, Bergmann's Rule is used to note that many, but not all, animals are larger in the northern portion of their range.

McLaren (1958, 1993) concluded that in northern regions with stable and persistent ice cover, individuals might have longer lactation periods and show better growth than ringed seals from more southerly areas with unstable, shifting ice cover. While the stability of the ice substrate, as it relates to the early development, growth, and survival of pups, may be important in local regions, it does not adequately explain differences in size over the wide range of latitude examined in this study. Stable fast ice is present in both Eureka and Arctic Bay, as well as in many protected areas near Pangnirtung and it persists until well after ringed seal pups are weaned. Seals from Arctic Bay would have equal opportunity for a complete lactation period as those from Eureka. Ringed seals occupying the pack ice of Baffin Bay, which have been postulated as a smaller ecotype, apparently maintain close mother-pup association on pack ice well into June (Finley et al. 1983). Unfortunately there are insufficient data available to test whether seals in northern regions actually exhibit a longer lactation period or are born longer than those in the south or of the pack ice. Another complication in this reasoning is the fact that juvenile seals often disperse into surrounding regions several hundred or even several thousand kilometers from where they were born (Smith 1973; Kapel et al. 1998). Therefore, asymptotic length, as influenced by ice substrate stability, would be representative of where the seals were actually born not where they currently reside.

Variation in patterns of growth can be seen in the shape of the growth curves and in age-specific plots of growth rate. Seals at Eureka had a higher rate of growth than Pangnirtung while the eventual decline in growth rate with age is similar in both locations (see Figure 2.4). This resulted in individuals in Eureka achieving a longer asymptotic length. In contrast, Arctic Bay has a rate of growth higher than both Eureka and Pangnirtung for the first 4 years of life. This rate of growth declines rapidly, falling below that of Pangnirtung by 6.5 years of age. Thus, seals in Arctic Bay reach 95% of their asymptotic length much sooner than in Eureka or in Pangnirtung but still have an asymptotic length intermediate between the two. It can be inferred from this high rate of growth that the age of sexual maturity may be less in Arctic Bay than the other sampling locations.

The data presented here suggest regional differences in growth and possible variation in general life history. It seems more plausible that a variety of factors including availability of food resources and predation pressure, rather than ice stability, exert selective pressures. The relationship between asymptotic length and primary production in each sampling location is not clear. Although dramatic reproductive failures linked to declines in resource availability have been observed in the western Canadian Arctic (Smith 1987), the cross-sectional nature of the data typically collected for marine mammals masks individuals which were stunted early in life and were more likely to die young. Most of the

curves presented here depict only the average size of individuals born over a 20-30 year period. It has been shown that the Lancaster Sound region adjoining Arctic Bay on Admiralty Inlet has a high rate of primary production relative to other areas of the arctic (Welch et al. 1992). In contrast to the western Arctic, no significant ringed seal population declines have been observed in this region (Furgal 1994). Although little is known about productivity in the high Arctic, it is thought that areas like Eureka have relatively low productivity. It should be noted however that seals in this region were very fat with high blubber depth/mass ratios for that time of year and stomachs containing amounts of digesta in excess of that which is typically observed for ringed seal (S. Innes, unpublished data and pers. com.).

Research into the population dynamics of northwest Atlantic harp seals suggests that age at sexual maturity, at which time most growth is complete, is linked to a density-dependent response, decreasing during periods of low population size (Capstick and Ronald 1982; Sjare et al. 1996). The fast growth evident in Arctic Bay may be due to an increased predation pressure exerted on the population by both polar bears and Inuit. Taylor and Lee (1995) divided the Canadian Arctic into 12 putative polar bear populations based on mark-recapture surveys and physical barriers to movement. The Queen Elizabeth Island region, containing Eureka had a polar bear density of 3.7 individuals per 1000 km², the Parry Channel region, encompassing Arctic Bay had 5.9/1000 km², and the

Davis Strait region including Pangnirtung had 2.3/1000 km². Thus, the density of polar bears is higher in mid-Arctic regions such as Arctic Bay than in Eureka or Pangnirtung (see also Stirling and Øritsland 1995) and this sampling location is subject to predation by hunters from the communities of Arctic Bay and nearby Nanisivik. Polar bear predation would be highest on pups and young-of-the-year exerting significant selection towards the rapid completion of juvenile growth. Although hunting pressure from humans in Pangnirtung is also very high, it is likely that most of the seals taken in that area of Cumberland Sound are smaller juveniles that have emigrated from unexploited populations in the Hoare Bay region (Smith 1973). Also, sampling conducted out of Pangnirtung encompassed a larger area with more variation in habitat than either Arctic Bay or Eureka. Seals in Eureka are not usually hunted by humans, predation by polar bears is slight, and this population is probably close to its carrying capacity. This observation is supported by the high age at which 95% of growth in length is achieved (10.4 years).

In the past, such differences in growth among locations would have been described in terms of classic r and K strategies (MacArthur and Wilson 1967). Characteristics of K-selected populations include slow development, delayed reproduction (sexual maturity), and larger body size while characteristics of r-selected populations include rapid development, early reproduction, and smaller body size (Pianka 1970). K-selected populations maximize long-term

reproductive efficiency while *r*-selected populations tend to favour increased productivity (Bernardo 1993). Current thinking, however, favours the view that animals mature along a dynamic trajectory of age and size that is influenced by population demographics, both environmentally and genetically determined (Stearns and Crandall 1984). These trajectories can be used to make testable quantitative predictions, allowing meaningful comparisons among or within species (Stearns and Koella 1986).

In summary, the present data suggests that observed differences in ringed seal growth in the Canadian Arctic may be a function of variation in life history strategy. Growth between the sexes in ringed seal varies only in the duration of growth and hence, the final adult size achieved. Finally, there is little evidence to suggest that the stability of the ice substrate, as it relates to pup growth, is responsible for significant differences in final adult length.

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CHAPTER THREE: SEASONAL CHANGES IN CONDITION INDICES OF RINGED SEALS (PHOCA HISPIDA)

Abstract

Morphometric data from 259 ringed seal (*Phoca hispida*) collected from Pangnirtung, NU in the eastern Canadian Arctic were examined to assess seasonal variation in condition. Condition was estimated using three published indices of condition: blubber thickness, axillary girth/length ratio, and the length-mass-fat depth (LMD) index. These indices did not adequately describe changes in condition and did not provide a precise measure of the absolute amount of fat present. A new method of estimating absolute sculp mass from sculp volume calculated by a prolate spheroid model was developed. Regressions of mass in relation to length for various seasons demonstrated that spring and summer mass loss averaged 14 kg for an adult seal 128 cm in length. Juveniles prior to sexual maturity lost less mass than adults. Utilization of blubber stores during periods of negative energy balance can be regarded as a balance between metabolic and thermoregulatory demands and the loss described can be maintained within the bounds of normal metabolic rates.

Introduction

In marine mammals, subcutaneous fat stores, or blubber, serve several important functions including insulating the body, providing energy for metabolism during periods of negative energy balance such as moult and lactation, increasing buoyancy, and improving streamlining (Scholander et al. 1950; Worthy and Lavigne 1983; Innes et al. 1990; Ryg et al. 1988, 1990a). In marine mammals, "condition" refers primarily to the amount of fat in the blubber layer. The interpretation of condition depends on the nature of the question being addressed. Biologists interested in thermoregulatory processes may be concerned with the relative thickness and topographical distribution of the blubber layer (Ryg et al. 1988) while other researchers may be more interested in the absolute amount of blubber available to meet energetic demands (i.e. Stewart and Lavigne 1984; Kovacs and Lavigne 1986).

Condition in ringed seal (*Phoca hispida*) has been assessed using xiphosternal blubber thickness, girth-to-length ratios, mid-dorsal blubber depth and the 'LMD' index (McLaren 1958; Ryg et al. 1990a). The 'LMD' index is an empirical equation that fits (length/mass)^{1/2} • blubber depth to blubber content as a percentage of total body mass. Xiphosternal blubber thickness and girth-to-length ratios are statistically insensitive to obvious states of malnutrition

(McLaren and Smith 1985). In addition, these indices reveal little about how much blubber a seal contains.

In this paper, morphometric data from ringed seals collected from Pangnirtung, NU, Canada between 1990 and 1996 were used to develop a means of estimating the absolute amount of blubber possessed by an individual using a geometric approximation. This method was compared to other published indices of condition calculated from the same data.

Methods and Materials

Morphometric measurements were made on ringed seals killed by Inuit between August 1990 and July 1996 from Pangnirtung on southeast Baffin Island. Animals were taken from leads or breathing holes during the winter and spring hunting season and from the open water during the summer and fall hunting season. Standard length and axillary girth (American Society of Mammalogists 1967) were each measured to the nearest centimeter, total body mass (including gut contents), sculp mass (skin plus blubber), and, in some cases, blubber mass (sculp minus skin) were recorded to the nearest kilogram. Xiphosternal blubber thickness was measured to the nearest millimeter using a steel tape measure inserted into a cut made through the skin. Ringed seal pups

exhibit rapid growth during their first year of life so for this reason only individuals older than one year were included in this study.

The three condition indices examined in this paper are: xiphosternal blubber thickness (cm), axillary girth (cm)/standard length (cm) • 100 (McLaren 1958), and the 'LMD'-index:

[1]
$$(L/M)^{1/2} \cdot d$$
,

where *L* is standard length in meters, *M* is total mass in kilograms, and *d* is blubber thickness in meters, measured dorsally at 60% of standard body length where it is most variable during the year (Ryg et al. 1990a).

Seasonal variation in blubber thickness, length/axillary girth • 100, and 'LMD' condition indices, calculated directly from the data, were compared as monthly means with corresponding 95% confidence intervals. Multiple comparisons of means were carried out using a one-way ANOVA model and Tukey's test (SPSSTM Ver. 6.1.3). The month of April contained only two data points and was excluded. These three methods of estimating condition were then compared against measured sculp mass expressed both in kilograms and as a percent of total body mass, as in Ryg et al. (1990a), to assess their predictive value. In addition, recorded sculp mass and total body mass, in kg,

were compared to sculp volume and total body volume, in m³, calculated from a general prolate spheroid model forced through the origin (Figure 3.1).

In this model, fd is the fat depth (measured at the xiphosternum), r is the core radius expressed in m (Swan 1974).

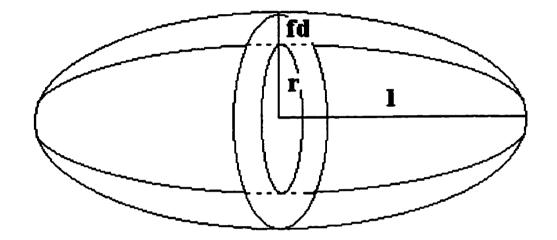
- [2] Total body volume (m³) = $4/3 \cdot \pi \cdot l \cdot (r+fd)^2$
- [3] Total fat volume (m³) = Total body vol. $4/3 \cdot \pi \cdot 1 \cdot r^2$

Seasonal patterns of mass change were examined by comparing the relationships between the log mass of individuals relative to their log length for each month. Differences among regression lines were tested using a general linear model (GLM) in SPSSTM Ver. 6.1.3 at a significance level of α=0.05 unless otherwise stated. A dummy variable representing the chosen time period (month, season, etc.) was introduced to the linear relationship of total body mass with respect to standard length. An interaction term between length and the time period was also incorporated into the model.

 $log Mass = B_0 + B_1(log length) + B_2(time period) + B_3(log length • time period)]$

The slopes of the regression were considered significantly different if the reduction in sum of squares error (SSE) between the full model (dummy variable

Figure 3.1. Prolate spheroid model used to relate volume of the whole seal and blubber layer to mass of each. /is ½ of standard length, fd is the xiphosternal fat depth, and r is radius of the core estimated from axillary girth and fat depth (all in cm).



= 1) and the reduced model (dummy variable = 0) was significant under the F-distribution (McClave and Dietrich 1994).

The effect of decreasing blubber depth on heat flow to the environment was estimated using a simple model representing heat loss across a cylindrical wall:

[4]
$$Q_{cyl} = 2\pi Lk(T_{bm}-T_a) / \ln(r_0/r_{bm})$$
 (Ryg et al. 1988)

,where:

 Q_{cyl} is heat flow (Watts)

L is standard length (m)

k is the thermal conductivity of the blubber layer (W m⁻¹ °C⁻¹)

T_{bm} is the temperature at the blubber/muscle interface (°C)

T_a is the ambient temperature (°C)

ro is the radius of the animal

r_{bm} is the radius of the core to the blubber/muscle interface.

Conductivity of the blubber was assumed to be 0.2 W m⁻¹ °C⁻¹ (Scholander et al. 1950), the temperature at the blubber/muscle interface was set 3° below a normal core temperature of 37° (Watts et al. 1993), and ambient temperature was fixed at -1.5° C, near the freezing point of seawater. Calculations were

based on an adult ringed seal 128 cm in length (asymptotic length for Pangnirtung, see Chapter Two) with a core radius of 11.45 cm and mass of 60 kg. Basal metabolic rate (BMR) was defined as 3.39 · Mass^{0.75} (Watts) (Kleiber 1975). The purpose of this exercise was to determine, in general terms, at what point blubber thickness decreases to the point were thermal balance can not be maintained at normal metabolic rates.

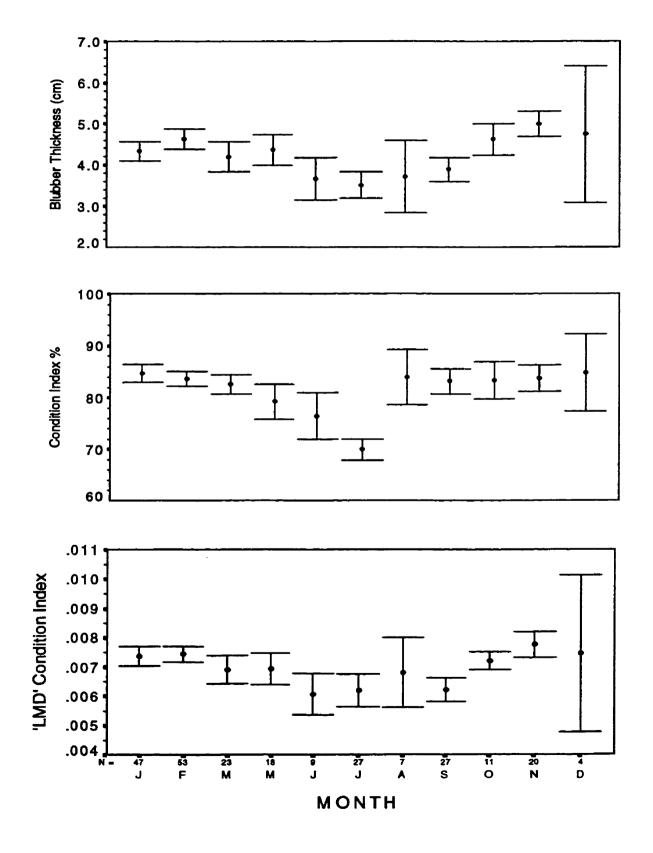
Results

No significant differences between the sexes were encountered during analysis although in some cases this was likely due to both small sample sizes and the inability to resolve subtle changes in the morphometric data, and measurement error.

Xiphosternal blubber thickness was relatively constant between December and May, ranging between means of 4.2 and 4.8 cm. Blubber thickness declined in June, reaching a minimum of 3.5 cm in July and then increased steadily to a yearly maximum of 5.0 cm in November (Figure 3.2). Blubber thickness in July was significantly lower than all months but August and December.

Mean % condition (girth/length X 100) ranged between 83 and 85% from November to February before beginning a gradual decline in March. A minimum

Figure 3.2. Mean monthly variation in A) xiphosternal blubber thickness, B) condition index axillary girth/length*100, and C) 'LMD' condition index (Ryg et al. 1990a). Bars represent 95% confidence intervals. April excluded due to small sample size



of 70% was reached in July. Mean condition in July was significantly lower than any other month. Condition was restored to winter levels by August and mean condition indices were similar until the following March.

The pattern of monthly variation in the 'LMD'-index was similar to that of the girth/length X 100 condition with the exception of a more gradual increase in condition in the fall and an unusual near-minimum drop during September. Both minimums in July and in September were significantly different than the high periods in November and January-February.

Xiphosternal blubber thickness, axillary girth/length index, and 'LMD'-index were all significantly correlated with sculp mass expressed both in kilograms and as a percent of total body mass. In all cases however, the coefficients of determination (r²) were poor (Table 3.1, Figures 3.3 - 3.5).

Both sculp mass and total mass were strongly correlated (p<0.0001) with sculp volume and total body volume calculated from the prolate spheroid model (Figure 3.6):

[5] Sculp mass (kg) = 794.69 • sculp volume (m³)
(
$$r^2 = 0.96$$
, $S_{xy} = 4.20$)

[6] Total mass (kg) = 838.48 • total body volume (m³)
(
$$r^2 = 0.98$$
, $S_{xy} = 5.53$)

Table 3.1. Results for regressions of sculp mass (kg) and sculp content (% of total body mass) on various indices of condition for ringed seals collected in Pangnirtung.

Regression Equation	r²	S _{xy}	p value
Sculp Mass = 4.95 • blubber thickness - 0.60	0.38	5.68	< 0.0001
Sculp Mass = 0.25 • condition index + 0.52	0.06	6.98	< 0.0001
Sculp Mass = 1088 • 'LMD' index + 12.98	0.03	7.07	< 0.01
Sculp Content = 2.23 • blubber thickness + 38.85	0.05	8.49	< 0.001
Sculp Content = 0.23 • condition index + 29.36	0.04	8.56	< 0.01
Sculp Content = 2078 • 'LMD' index + 33.81	0.08	8.36	< 0.0001

Figure 3.3. Relationship of A) sculp content (% of total mass) and B) sculp mass (kg) to xiphosternal blubber thickness in ringed seals collected from Pangnirtung.

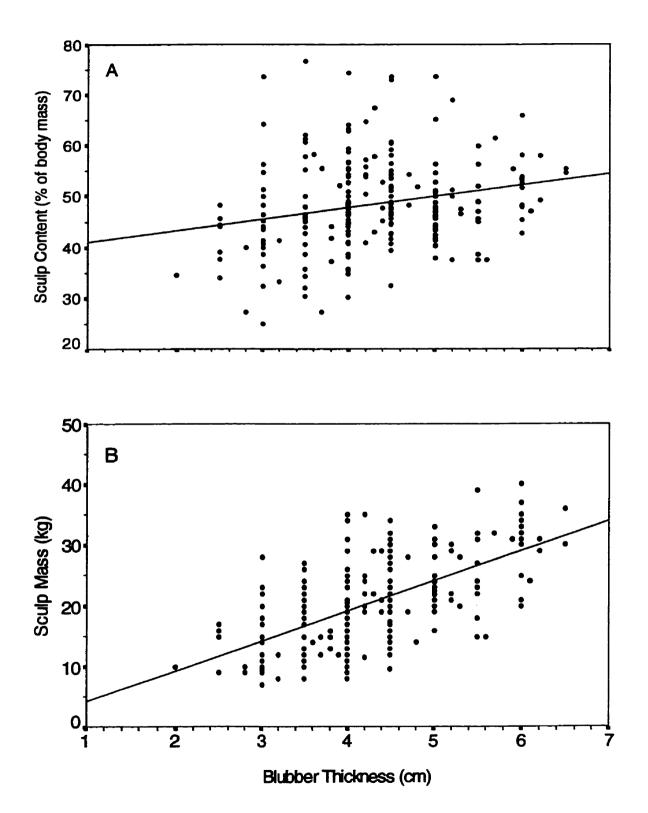


Figure 3.4. Relationship of A) sculp content (% of total mass) and B) sculp mass (kg) to condition index (axillary girth/length *100) in ringed seals collected from Pangnirtung.

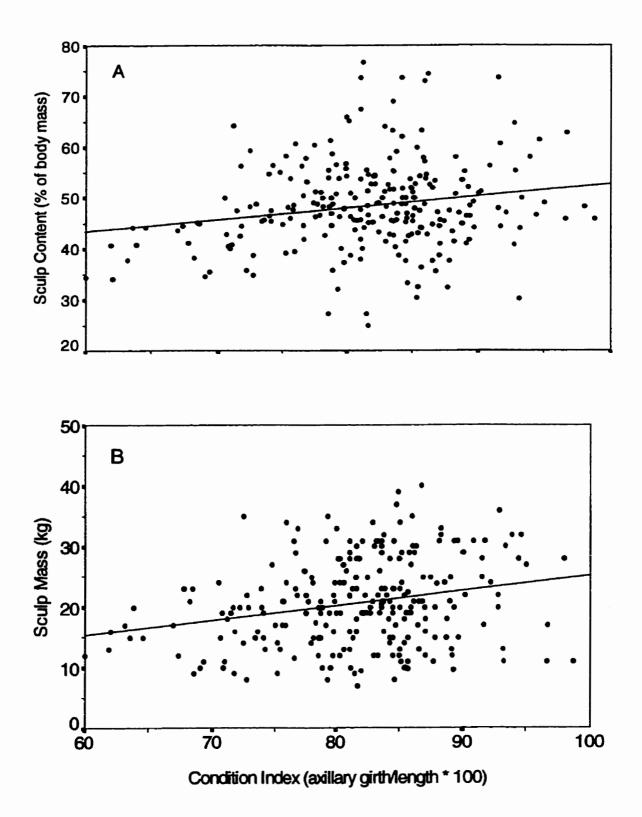


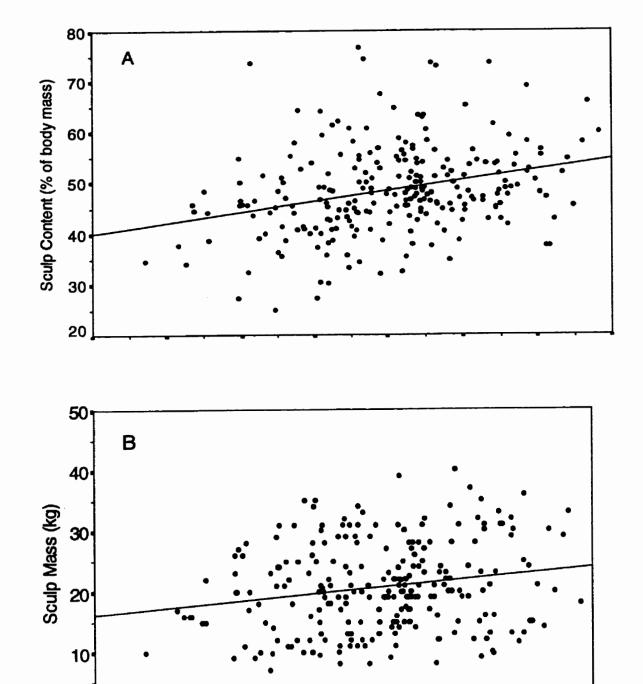
Figure 3.5. Relationship of A) sculp content (% of total mass) and B) sculp mass (kg) to 'LMD' index (length/mass^{1/2} * blubber thickness) in ringed seals collected from Pangnirtung.

.

.009

.008

.010



.003

.005

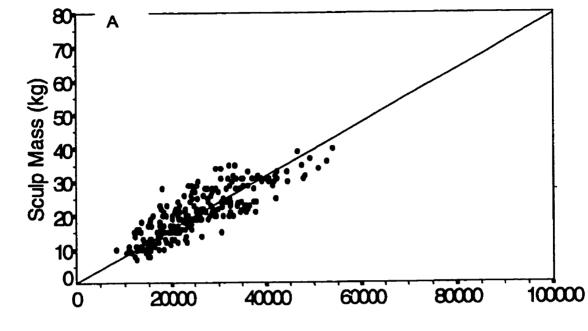
.004

.006

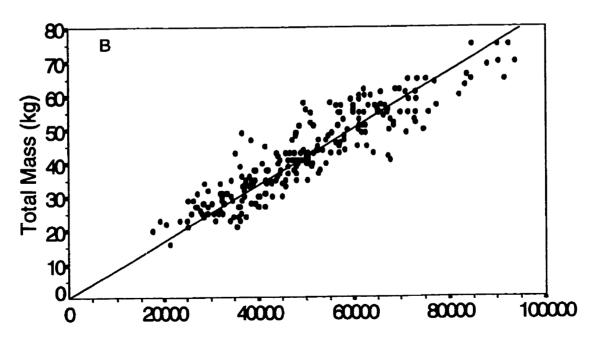
'LMD' Index

.007

Figure 3.6. Relationship of A) sculp mass (kg) and B) total body mass (kg) to volume (cc) predicted from the prolate spheroid model. Regression forced through the origin in both cases.



Sculp Volume Calculated From the Prolate Spheroid Model (cc)



Total Body Volume Calculated from the Prolate Spheroid Model (cc)

The slopes of the predicted regression lines were significantly different from 1000 (p<0.01) ruling out a direct mass to volume relationship between the mass of the seal and its blubber volume predicted from length and girth.

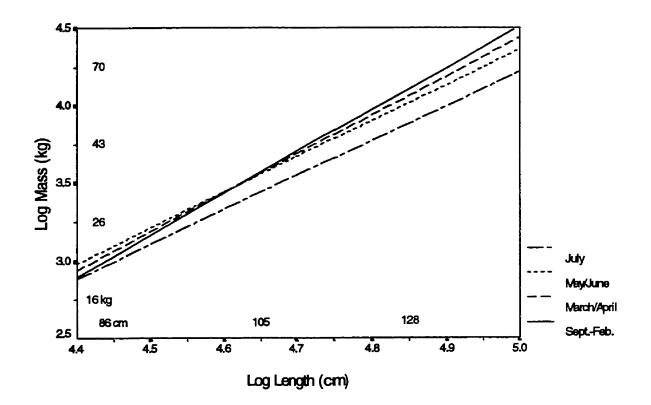
Condition was relatively constant September through February and the mass-length regression for this period was used as a 'standard' by which to compare mass changes during the period March through July when condition declined. This period was broken down into the following blocks: pupping - March/April, haul out and moult - May/June, and minimum condition in July, to increase sample sizes. There was a decrease in the predicted mass-length ratio for each period following the September through February 'standard' mass-length regression (Figure 3.7).

Change in mass from peak condition to minimum condition was then estimated by comparing the mass-length relationships for the month of January (peak condition) and July (minimum condition).

[7] log Total mass (January) = log length • 2.91 - 9.95
(
$$r^2 = 0.74$$
, $S_{xy} = 0.16$)

[8] log Total mass (July) = log length • 2.23 - 6.90
$$(r^2 = 0.80, S_{xy} = 0.13)$$

Figure 3.7. Mass-length regressions for ringed seals collected from Pangnirtung during the periods September - February, March/April, May/June, and July.



Estimated weight loss for an adult ringed seal 128 cm in length, based on the difference between the expected mass-length regression in July versus January, is 14.4 kg representing a 22.7% mass loss (Figure 3.8). Assuming that the bulk of this mass loss occurs from the beginning of the breeding season in early March to the completion of moult in late June, this represents a daily mass loss of about 120 g/day. Sexually immature animals also lost mass during this period but at age six (114 cm, see Chapter 2), just prior to sexual maturity in males and first reproduction in females, mass loss was only 7.42 kg, half that of adults and representing only a 16.4% total mass loss.

Significant individual variability was evident with large 95% prediction intervals. There was no indication of seasonal fluctuations in core mass so it was assumed that mass was lost primarily from the blubber layer.

Heat flow calculations resulted in a curvilinear relationship of decreasing heat flow with increasing blubber thickness (Figure 3.9).

Figure 3.8. Regression of log body mass on log standard body length of ringed seals collected from Pangnirtung during maximum condition (January, solid line) and minimum condition (July, dotted line). Sexual maturity set at 117 cm (size at age 7 for this population). Regression lines differed significantly (p<0.0001).

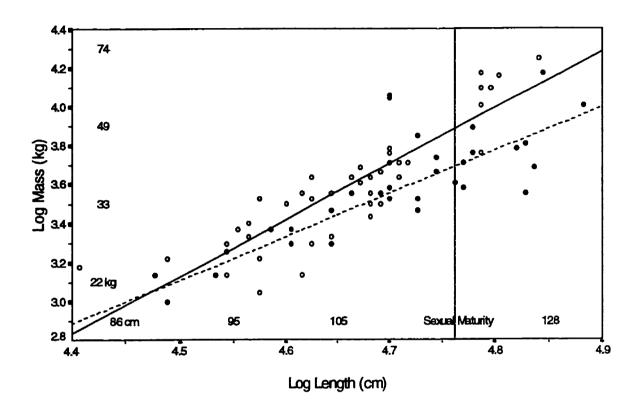
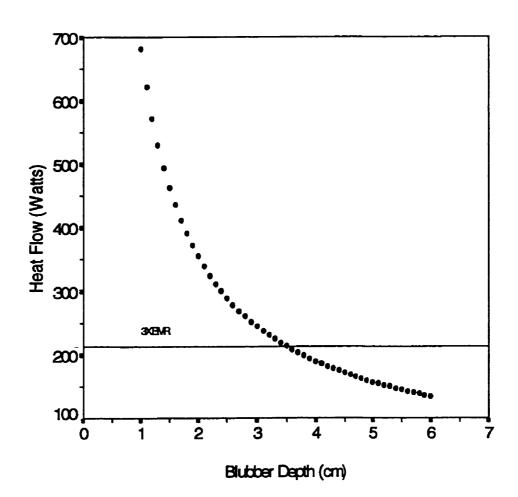


Figure 3.9. Heat flow (Watts) of an adult ringed seal 128 cm in length with a mass of 60 kg decreases with increasing blubber depth (cm). See text for model details.



Discussion

Variation in Condition Indices

Ryg et al. (1990a) found significant correlation between blubber content (as a percent of body mass) and the girth/length X 100 condition index (p<0.01, r^2 =0.39, S_{xy} =5.17) and between blubber content and the 'LMD' index (p<0.01, r^2 =0.82, S_{xy} =2.80) for ringed seals collected in the Barents Sea and Svalbard. Although results from the present study were similarly correlated, there was a greater degree of variability in the data as evidenced by the lower r^2 values for the axillary girth/length X 100 and the 'LMD' indices. There are several possible reasons for this variability. There may have been measurement error in total mass and sculp mass, modification of 'LMD' index parameters because of how the data were collected, and natural variation in condition for this population.

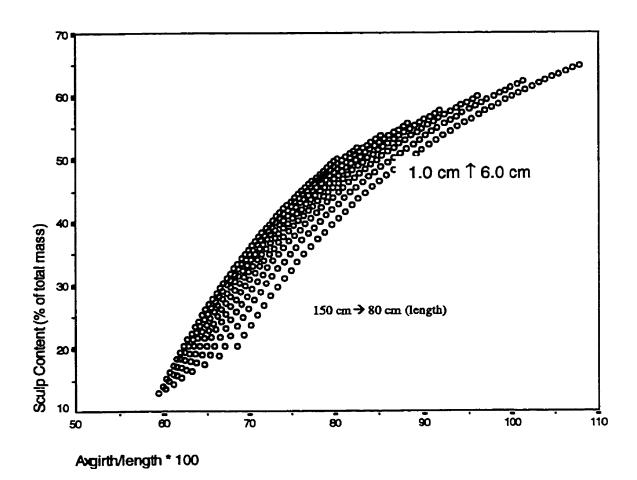
Variation of the magnitude indicated by the data, upwards of ten or more kilograms is unlikely to be the result of simply an inaccurate or imprecise scale. The scale used was accurate to +/- 2 kg. according to the manufacturers specifications. In the present study, several modifications were made to the parameters of the 'LMD' index for logistic reasons that may have increased variability and reduced its predictive value. Because it was impractical for

hunters to thoroughly dissect out the fat from the skin while hunting, percent sculp (blubber layer including the skin but not the flippers) rather than percent of actual blubber was used in the calculation of the 'LMD' index. Also, the location for measuring blubber depth specified by Ryg et al. (1990a) for the 'LMD' index was dorsally at about 60% of standard length where blubber depth varies the most as mass changes. A dorsal measurement would ruin the pelt, so xiphosternal blubber thickness was substituted and sculp mass was substituted for fat mass. These were most likely sources of variation. Alternatively, there may be a high degree of natural variability present in this ringed seal population. Variability in adult body length varies throughout the ringed seals' range but is highest in the Canadian Arctic (McLaren 1993; Chapter 2). Even so, the 'LMD' index should have captured this variation if it is an accurate estimator of condition.

Girth/length condition indices have been criticized as being insensitive to individuals near death from starvation (Smith 1987). Figure 3.10 clearly illustrates that this index is not a linear estimator of percent blubber content even within the narrow range of typical ringed seal body lengths. Differences in condition can only be suitably compared when length is constant or suitably accounted for. Longer animals have a geometrically smaller percent of blubber which results in a smaller range of condition values. This means that a large seal would not necessarily be in poorer condition than a smaller seal with a much

Figure 3.10. The axgirth/length*100 condition index is not a linear estimator.

Each curve represents a 10 cm decrease in length left to right and a 1 mm increase is blubber thickness bottom to top.



higher condition index. The advantage of the girth/length index is that the seal does not need to be killed (i.e. to measure fat depth) but without weighing the animal, which can require considerable effort, percent blubber is meaningless.

The 'LMD' index may also suffer from a degree of nonlinearity, although not as marked as with girth/length indices. Ryg et al. (1990a) found that for the range of phocid seals between 80 cm (young ringed seal) and 230 cm (adult male grey seal) this estimator worked reasonably well. It should be noted however that outside this range (i.e. the full range of seals from ringed seal to elephant seal) nonlinearity increases and suggests that for larger animals the 'LMD' index, as parameterized by Ryg et al. (1990a), does not hold. This estimator also requires weighing of the animal and the pelt-destroying measurement of dorsal blubber thickness, or the use of equipment such as ultrasound (Gales and Burton 1987).

Assuming percent blubber can be shown to be well correlated with the girth/length ratio and 'LMD' condition indices, both suffer from an inability to accurately represent the absolute amount of fat a seal actually contains. The 'LMD' estimator, as used by Ryg et al. (1990a) regresses fat content (as a percentage of total mass) on the 'LMD' index which also contains a total mass variable thus confounding the relationship between the index and blubber mass. To estimate total blubber mass, the I dimension will have to be modified. Clearly, these indices did not adequately describe condition for the present data and an

alternative means of describing condition in terms of absolute amount of fat was needed.

Sculp mass and total body mass were well described by the prolate spheroid models. These measures relate the weight of the sculp in familiar units that may be used in the computation of thermoregulatory and energetic formulae. It does not require the cumbersome and often inaccurate weighing of the animal to estimate the animals condition. Most pinnipeds should be geometrically approximated by the generalized prolate spheroid model. This method would be extremely useful when dealing with large pinnipeds such as the elephant seal or walrus where weighing is logistically difficult (Garlich-Miller and Stewart 1998). However, validation of this model with larger pinniped species is still required.

Energetics of Condition

The mass loss estimate of 120 g/day from this work is similar to the 100g/day mass loss for males and 160 g/day mass loss for females during the same period reported for the Svalbard Islands (Ryg et al. 1990b). So, while it can be shown that an adult ringed seal loses, on average, 14 kg between early March and late June it is difficult to estimate the energetic demands of any particular component of the individual's energy budget. The period between

March and August represents a period of decreased feeding activity and increased energetic expenditure related to territorial defense and intraspecific aggression in males, lactation in females, and annual mating and moulting in both sexes. The annual pattern of mass change in ringed seal has been well documented by both field observation and theoretical modelling (Smith 1987; Ryg et al. 1990b; Ryg and Øritsland 1991) and agrees well with data from the present study. Mass loss begins during the pupping season in March concomitant with the establishment of breeding territories by males. Weight loss peaks in July, following the moult in May/June, before both sexes replenish their energy reserves in August and September. Mass is quickly restored to near peak levels by the end of September. That juveniles exhibit a lower rate of mass loss than adults is not surprising considering they do not participate in most activities associated with reproduction until they have achieved sexual maturity. However, these animals do undergo an annual moult.

As fat reserves are depleted there will come a time when blubber thickness will be insufficient to maintain thermorieutrality. For example, 1.5 cm is likely the minimum blubber thickness, below which insulation is insufficient for maintaining thermoneutrality in young harbour seals (Worthy 1991). Ryg et al. (1988) concluded that while there were differences in the topographical distribution of blubber, with the hind parts being "overinsulated", the ratio of

blubber thickness to body ratio was nearly constant maximizing insulative properties. They argue that during starvation, thermoregulatory difficulties could be minimized by simultaneously losing mass from the core. In a later paper (Ryg et al. 1990b) however, no evidence indicating significant mass loss from the core was found. It does not appear that the majority of seals in the present study showed reductions in blubber thickness that would indicate a negative thermal balance. Average blubber thickness decreased by approximately 1.5 cm from a winter maximum of 5.0 cm to summer minimum of 3.5 cm. Heat flow calculations suggest that a seal with a minimum July blubber thickness of 3.5 cm could maintain thermal balance if its metabolism produced heat at about 2.7X BMR (Figure 3.9). While this rate may seem high but it is not unreasonable considering that this heat loss occurs in water and during the annual moult in June most seals bask on the ice surface for long periods. Also, unlike other phocids, ringed seals do not suspend feeding during the moult but may only reduce their food intake due to the amount of time spent on the ice (Lowry et al. 1980). Innes et al. (1987) found that the rate of energy ingestion (IE) required for the maintenance of adult phocid seals was 7.10 · Mass^{0.72} (Watts) or about 2.1 X BMR as defined earlier. Thus, it seems that for most of the year, ringed seals maintain thermoneutrality within the bounds of normal metabolism.

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GENERAL SUMMARY

It is clear that significant regional variation in the size of ringed seal exists throughout the Canadian Arctic. The next logical step in ringed seal research is the integration of growth, with respect to both size and pattern, and condition, in terms of meeting energetic and thermoregulatory demands of that body size. This approach is fundamental to the development of an underlying evolutionary theory explaining these differences in size. This will require the collection and analysis of both current and future data detailing a wider range of morphometric and life-history characteristics as well as detailed information about the seals' habitat. From this data it may be possible to elucidate correlation between one or several of these traits and body size.

Changes in condition are important because they are not only potential indicators of the seals' overall health but indicators of the productivity of the environment, the effects of climatic warming trends, and major predators such as the polar bear. This thesis has demonstrated that current methods of estimating condition are, at best, crude. Issues such as natural variability, measurement error, and small sample sizes are all major stumbling blocks. Indeed, it may be that these concerns will never be resolved given the cost and logistic difficulties involved in data collection in the far north.

Future research priorities should focus on general reproductive biology to determine if the observation that sexual maturity may occur later in some regions is corroborated by reproductive tract analysis. Given the importance of the ringed seal to Inuit, such aspects of population ecology must be better understood.

APPENDIX I: RINGED SEAL MORPHOMETRIC DATA

Sample	<u>Sex</u>	<u>Day</u>	<u>Month</u>	<u>Year</u>	<u>Age</u>	<u>Ageadi</u>	Mass	<u>Length</u>	<u>Axgirth</u>	Blubber	Sculpmass	<u>Fatmass</u>
AREU94-01	F	31	5	1994	3	3,167	55.0	117.0	96.0	3.6	21	13
AREU94-02	M	31	5	1994	8	8.167	114.0	151.0	123.0	3.3	42	23
AREU94-03	M	1	6	1994	21	21.170	106.0	147.0	117.0	4.0	37	22
AREU94-04	M	1	6	1994	2	2.170	31.0	102.0	75.0	2.0	•	•
AREU94-05	F	2	6	1994	14	14.173	100.0	146.0	119.0	4.6	43	29
AREU94-06	M	2	6	1994	14	14.173	120.0	155.0	125.0	5.0	41	25
AREU94-07	M	2	6	1994	7	7.173	72.0	143.0	98.0	2.9	•	•
AREU94-08	M	3	6	1994	0	0.175	38.0	106.0	93.0	4.0	•	•
AREU94-09	F	3	6	1994	38	38.175	113.0	151.0	119.0	4.6	38	23
AREU94-10	F	4	6	1994	18	18.178	90.0	147.0	108.0	2.2	30	19
AREU94-11	F	4	6	1994	16	16.178	64.0	137.0	93.0	2.9	31	21
AREU94-12	F	4	6	1994	0	0.178	36.0	99.0	85.0	3.2	•	•
AREU94-13	F	4	6	1994	0	0.178	34.0	91.0	82.0	3.9	•	•
AREU94-14	F	5	6	1994	33	33.181	86.0	146.0	103.0	2.1	28	17
AREU94-32	M	28	5	1994	0	0.159	32.0	94.0	84.0	2.5	18	•
AREU94-33	F	30	5	1994	32	32.164	117.0	159.0	117.0	3.1	40	27
AREU94-35	F	30	5	1994	19	19.164	129.0	153.0	136.0	4.8	54	40
AREU94-36	M	30	5	1994	6	6.164	75.0	121.0	110.0	3.4	30	20
ARAB93-01	F	13	4	1993	•	0.036	8.0	70.0	48.0	2.0		•
ARAB93-02	F	16	4	1993	•	0.044	14.0	76.0	56,0	1.0		•
ARAB93-03	F	19	4	1993	12	12.052	83.0	129.0	116.0	6.0	•	•
ARAB93-04	F	19	4	1993	•	0.052	7.0	70.0	50.0	1.0	•	•
ARAB93-05	F	19	4	1993		0.052	13.0	72.0	60.0	2.2	•	
ARAB93-06	F	20	4	1993	•	0.055	15.0	84.0	61.0	2.3	•	•
ARAB93-07	F	21	4	1993	8	8.058	85.0	132.0	125.0	4.0	•	•

ARAB93-08	F	21	4	1993		0.058	9.0	70.0	53.0	1.0		
ARAB93-09	M	21	4	1993	•	0.058	9.0	68.0	47.0	1.1	•	•
ARAB93-10	F	1	5	1993	3	3.085	39.0	105.0	89.0	3.5		
ARAB93-11	М	1	5	1993	7	7.085	73.0	124.0	115.0	4.5	•	
ARAB93-12	M	1	5	1993	21	21.085	70.0	127.0	107.0	3.2		•
ARAB93-13	M	5	5	1993	3	3.096	51.0	109.0	103.0	5.1	•	•
ARAB93-14	M	5	5	1993	8	8.096	122.0	129.0	113.0	4.8		
ARAB93-16	M	13	5	1993	4	4.118	60.0	128.0	108.0	4.5	•	
ARAB93-17	M	15	5	1993	9	9.123	108.0	152.0	124.0	5.0	•	•
ARAB93-18	M	16	5	1993	12	12.126	101.0	156.0	126,0	3.5		
ARAB93-19	M	18	5	1993		0.132	22.0	87.0	78.0	3.5		•
ARAB93-20	M	18	5	1993	7	7.132	65.0	131.0	108.0	5.0	•	
ARAB93-21	M	20	5	1993	20	20.137	45.0	133.0	89.0	2.5	•	
ARAB93-22	M	22	5	1993		0,142	23.0	90.0	73.5	4.0	•	
ARAB93-23	F	22	5	1993		0.142	22.0	84.0	74.0	3.0	•	
ARAB93-24	F	23	5	1993	1	1.145	35.0	107.0	91.0	4.0	•	
ARAB93-25	M	25	5	1993	2	2.151	48.0	104.0	104.0	5.5	•	•
ARAB93-26	F	26	5	1993	15	15.153	94.0	145.0	126.0	5.0	•	
ARAB93-27	F	26	5	1993	4	4.153	59.0	123.0	107.0	5.8		
ARAB93-28	F	27	5	1993		0.156	21.0	90.0	74.0	4.0	•	
ARAB93-29	F	27	5	1993	3	3.156	56.0	127.0	98.0	5.0	•	
ARAB93-30	M	28	5	1993	9	9.159	68.0	133.0	107.0	3.0		
ARAB93-31	F	29	5	1993	4	4.162	26.0	95.0	84.0	4.0	•	
ARAB93-32	M	30	5	1993	12	12.164	61.0	125.0	105.0	5.5	•	
ARAB93-33	M	30	5	1993	6	6.164	71.0	133.0	115.0	6.2	•	
ARAB93-34	F	2	6	1993	5	5.173	53.0	116.0	100.0	4.0	•	
ARAB93-35	F	2	6	1993	5	5.17 3	61.0	128.0	108.0	5.0	•	•
ARAB93-36	M	3	6	1993	•	0.175	34.0	90.0	87.0	5.0	•	•
ARAB93-37	M	3	6	1993	•	0.175	36.0	96.0	89.0	5.2	•	•
ARAB93-38	F	3	6	1993	•	0.175	30.0	95.0	87.0	5.5	•	•
ARPG90-01	F	29	8	1990	4	4.414	30.0	105.0	90.0	4.0	19	

ARPG90-02	M	29	8	1990	1	1.414	28.0	93.0	76.0	3.0	7	•
ARPG90-03	F	29	8	1990	1	1.414	21.0	89.0	73.0	3.0	9.5	•
ARPB90-04	M	29	8	1990	3	3.414	25.0	90.5	73.5	2.8	10	•
ARPG90-05	F	31	8	1990	1	1.419	23.0	105.0	80.5	4.2	11.6	•
ARPG90-06	M	31	8	1990	2	2.419	28.0	102.0	84.2	4.6	27	•
ARPG90-07	M	31	8	1990	6	6.419	55.0	102.0	97.0	5.5	27	•
ARPG90-08	M	3	9	1990	5	5.427	58.0	102.5	100.5	4.7	28	•
ARPG90-09	F	4	9	1990	7	7.430	53.0	122.0	94.5	4.0	26	•
ARPG90-10	F	5	9	1990	2	2.433	33.0	103.0	84.0	2.8	9	•
ARPG90-11	M	6	9	1990	0	0.436	22.0	86.0	74.0	3.5	8.6	•
ARPG90-12	F	6	9	1990	1	1.436	43.0	94.0	84,0	3,5	20	•
ARPG90-13	F	6	9	1990	5	5.436	57.0	115.0	96.0	3.5	26	•
ARPG90-14	М	7	9	1990	5	5.438	59.0	121.0	97.5	3,5	27	•
ARPG90-15	M	10	9	1990	7	7.447	61.0	119.0	106.0	4.2	25	
ARPG90-16	M	12	9	1990	5	5.432	60,0	109.5	103.5	4.5	28	•
ARPG90-17	M	12	9	1990	8	8.432	62.0	122.0	98.0	4.0	24	•
ARPG90-18	М	13	9	1990	6	6.455	59.0	114.0	99.0	4.0	21	
ARPG90-19	M	13	9	1990	2	2.455	24.0	98.0	83.0	3.2	8	•
ARPG90-20	M	13	9	1990	10	10.455	61.0	129.0	98.0	4.5	24	•
ARPG90-21	M	15	9	1990	1	1.460	29.0	97.0	82.0	3.2	12	
ARPG90-22	F	18	9	1990	0	0.486	36.0	103.0	79.0	3.0	12	•
ARPG90-23	M	18	9	1990	2	2.468	31.0	101.0	79.0	2.5	15	•
ARPG90-24	M	19	9	1990	7	7.471	47.0	118.0	93,0	4.0	21	•
ARPG90-25	F	19	9	1990	3	3.471	43.0	103.0	96.0	4.0	13	•
ARPG90-26	M	20	9	1990	1	1.474	31.0	99.0	79.5	3.5	12	•
ARPG90-27	M	20	9	1990	4	4.474	47.0	130.0	92.0	4.0	11	•
ARPG90-28	M	20	9	1990	4	4.474	70.0	134.5	117.0	5.2	15	•
ARPG90-29	F	22	9	1990	4	4.479	42.0	110.0	93.0	4.4	19	•
ARPG90-30	F	22	9	1990	2	2,479	44.0	117.0	92.0	3.7	12	
ARPG90-31	M	24	9	1990	0	0.485	23.0	88.5	75.0	4.2	11	•
ARPG90-32	M	24	9	1990	0	0.485	26.0	94.5	7 3.5	2.7	12	
ARPG90-33	F	25	9	1990	3	3.485	43.0	109.0	87.0	3.8	16	

ARPG90-34	M	28	9	1990	1	1.493	23.0	84.0	75.0	4.5	9.6	
ARPG90-35	F	29	9	1990	1	1.496	27.0	91.0	78.0	3.0	9.8	•
ARPG90-36	M	7	11	1990	0	0.605	27.0	85.5	79,5	4.0	14	
ARPG90-37	M	7	11	1990	0	0.605	22.5	90.0	71.0	3.7	12	•
ARPG90-38	F	7	11	1990	0	0.605	24.0	87.2	77.0	4.2	13	•
ARPG90-39	М	7	11	1990	0	0.605	21.5	94.7	66.0	2.8	10	
ARPG90-40	M	7	11	1990	0	0.605	39.0	91.3	83.4	4.7	15	
ARPG90-41	F	8	11	1990	0	0.608	23.5	85.0	76.0	4.0	7	
ARPG90-42	F	8	11	1990	0	0.608	36.0	99.0	89.0	4.5	18	
ARPG90-43	M	12	11	1990	3	3.619	44.0	109.0	95.0	4.0	18	•
ARPG90-44	M	12	11	1990	0	0.619	26.0	89.0	79.0	4.0	13	
ARPG90-45	F	12	11	1990	0	0.619	24.0	82.0	78.5	3.5	13	•
ARPG90-46	M	14	11	1990	3	3.625	51.0	113.2	97.0	5.0	22.5	
ARPG90-47	M	14	11	1990	6	6.625	57.5	123.5	100.2	5.0	21.8	
ARPG90-48	M	14	11	1990	1	1.625	31.0	102.0	70.7	4.0	11	•
ARPG90-49	M	14	11	1990	9	9.625	56.0	119.0	103.0	5.2	21	•
ARPG90-50	М	19	11	1990	0	0.638	17.4	88.8	68.0	2.0	7	
ARPG90-51	M	19	11	1990	7	7.638	55.0	117.0	103.0	5.0	23.9	•
ARPG90-52	F	1	1	1991	7	7.756	64.0	122.0	109.0	4.5	31	
ARPG90-53	M	2	1	1991	5	5.759	43.0	120.0	93.0	4.5	26	•
ARPG90-54	M	3	1	1991	4	4.762	70.0	126.5	116.0	5.0	31	
ARFG90-55	M	4	1	1991	0	0.764	27.0	88.0	84.0	4.0	12	•
ARPG90-56	F	5	1	1991	2	2.767	39.0	109.0	94.0	4.0	29	•
ARPG90-57	F	7	1	1991	4	4.773	38.0	106.0	97.0	5.0	28	
ARPG90-58	F	8	1	1991	1	1.775	25.0	89.0	83.0	3.5	11	•
ARPG90-59	F	9	1	1991	0	0.778	25.0	87.0	83.5	4.0	10	•
ARPG90-60	F	10	1	1991	1	1.781	24.0	82.0	81.0	3.5	11	
ARPG90-61	F	15	1	1991	2	2.795	33.0	99.5	85.0	3.5	10	•
ARPG90-62	M	16	1	1991	2	2.797	28.0	96.0	88.0	3,5	17	
ARPG90-63	F	17	1	1991	3	3.800	37.0	107.0	92.0	4.5	27	
ARPG90-64	F	18	1	1991	0	0.803	23.0	86.0	81.0	4.0	11	
ARPG90-65	М	19	1	1991	1	1.805	58.0	110.0	92.0	4.5	30	•

ARPG90-66	F	22	1	1991	0	0.814	27.0	93.0	81.0	3,5	15	
ARPG90-67	M	23	1	1991	3	3.816	38.0	108.0	91.0	4.5	28	
ARPG90-68	F	25	1	1991	4	4.822	57.0	110.0	99.0	4.0	29	
ARPG90-69	М	28	1	1991	0	0.830	27.0	94.0	86.0	4.5	15	
ARPG90-70	F	29	1	1991	0	0.833	28.0	95.0	87.0	3.5	16	
ARPG90-71	M	30	1	1991	2	2.836	27.0	94.0	91.0	4.0	17	
ARPG90-72	F	31	1	1991	1	1.838	38.0	111.0	90.0	3.0	28	•
ARPG92-02	F	16	10	1992	6	6.545	46.0	114.0	96.4	5.0	23	
ARPG92-03	М	16	10	1992	4	4.545	43.0	112.0	89.5	4.2	24	•
ARPG92-04	F	27	10	1992	4	4.575	55.0	122.0	98.0	5.0	28	•
ARPG92-05	F	27	10	1992	2	2.575	37.0	109.5	87.5	4.0	21	•
ARPG92-06	F	28	10	1992	5	5.578	41.0	111.0	90.0	4.5	22	•
ARPG92-07	F	28	10	1992	5	5.578	55.0	129,0	99.0	5.0	23	-
ARPG92-08	M	13	11	1992	8	8.622	42.0	122,0	102.0	5.2	29	
ARPG92-09	M	13	11	1992	3	3.622	48.0	116.0	97.0	4.0	20.5	
ARPG92-11	M	13	11	1992	15	15.622	70.0	133.0	116.0	5.0	41	
ARPG92-12	F	13	11	1992	8	8.622	62.0	130.0	100.0	6.0	33	
ARPG92-13	F	13	11	1992	14	14.622	50.0	130.0	104.0	6.0	33	•
ARPG92-14	F	13	11	1992	3	3.622	47.0	116.0	97.0	5.5	23	
ARPG92-15	F	16	11	1992	11	11.630	51.0	114.0	101.0	6.1	24	
ARPB92-16	M	16	11	1992	5	5.630	48.0	119.0	93.0	5.0	24	•
ARPG92-17	F	16	11	1992	7	7.630	43.0	114.0	97.0	5.0	20	
ARPG92-18	M	16	11	1992	10	10.630	65.0	133.0	102.0	4.5	29	
ARPG92-10	M	2	2	1993	0	0.844	33.0	109.0	80.0	3.8	20	
ARPG92-19	F	29	1	1993	3	3.833	40.0	107.0	94.0	5.6	15	•
ARPG92-20	M	29	1	1993	0	0.833	28.0	98.0	74.0	3,5	9	
ARPG92-21	F	29	1	1993	2	2.833	25.0	97.0	77.0	3.5	8	•
ARPG92-22	M	29	1	1993	2	2.833	35.0	104.0	89.0	4.2	19	
ARPG92-23	M	30	1	1993	2	2.836	29.0	95.0	80.0	3,5	18	•
ARPG92-24	M	30	1	1993	2	2.836	34.0	97.0	90.0	4.2	22	•
ARPG92-25	M	30	1	1993	2	2.836	28.0	104.0	74.0	3.0	18	

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ARPG92-58	M	10	2	1993	3	3.866	38.0	108.0	83.0	4.3	22	•
ARPG92-59	F	10	2	1993	4	4.866	45.0	119.0	98.0	4.5	22	•
ARPG92-60	M	12	2	1993	2	2.871	43.0	126.0	98.0	5.0	21	•
ARPG92-61	M	12	2	1993	3	3.871	24.0	105.0	79.0	3.6	14	•
ARPG92-62	F	12	2 2	1993	4	4.871	30.0	102.0	86.0	4.0	15	•
ARPG92-63	M	12	2	1993	2	2.871	27.0	99.0	83,0	4.5	16	•
ARPG92-64	F	12	2	1993	1	1.871	27.0	103.0	81.0	3.7	15	•
ARPG92-65	M	12	2	1993	8	8.871	45.0	114.0	97.0	4.5	23	•
ARPG92-66	M	12	2	1993	4	4.871	34.0	105.0	90.0	4.0	15	•
ARPG92-67	F	12	2	1993	7	7.871	53.0	127.0	104.0	5.0	28	•
ARPG92-68	F	12	2	1993	5	5.871	33.0	109.0	89.0	4.0	16	•
ARPG92-69	M	12	2	1993	8	8.871	75.0	136.0	118.0	6.0	40	•
ARPG92-70	F	12	2	1993	6	6.871	63.0	125.0	112.0	6.2	31	•
ARPG92-71	F	12	2	1993	12	12.871	59.0	138.0	100.0	4.0	35	•
ARPG92-72	М	12	2	1993	9	9.871	65.0	129.0	111.0	6.0	35	
ARPG92-73	F	12	2	1993	7	7.871	50.0	120.0	103.0	6.2	29	•
ARPG92-74	F	13	2 2	1993	8	8.874	65.0	126.0	117.0	6.5	36	•
ARPG92-75	F	13	2	1993	2	2.874	37.0	115.0	87.0	3.5	17	•
ARPG92-76	F	13	2	1993	4	4.874	35.0	112.0	92.0	4.0	19	•
ARPG92-77	F	13	2	1993	7	7.874	45.0	116.0	101.0	5.0	20	•
ARPG92-78	M	26	2	1993	7	7.910	54.0	120.0	102.0	4.5	28	•
ARPG92-79	M	26	2	1993	7	7.910	61.0	130.0	103.0	5.0	31	•
ARPG92-80	F	26	2	1993	1	1.910	30.0	100.0	78.0	4.0	14	•
ARPG93-01	F	4	5	1993	1	1.093	51.0	120,0	99.0	4.0	25	_
ARPG93-02	M	4	5	1993	12	12.093	65.0	131.0	104.0	4.2	35	·
ARPG93-03	F	4	5	1993	5	5.093	50.0	115.0	98,0	5.0	24	•
ARPG93-04	F	4	5	1993	5	5.093	55.0	122.0	104.0	4.4	29	
ARPG93-05	F	5	5	1993	2	2.093	43.0	111.0	90.0	4.3	29	•
ARPG93-06	M	5	5	1993	2	2.093	43.0	111.0	89.0	5.0	28	•
ARPG93-07	M	5	5	1993	4	4.093	43.0	102.0	92.0	5.2	22	•
ARPG93-08	M	5	5	1993	3	3.093	49.0	114.0	89.0	5.0	25	•
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ARPG93-09	M	27	5	1993	2	2.156	38.0	104.0	87.0	4.0	21	
ARPG93-10	М	27	5	1993	1	1.156	35.0	105.0	84.0	4.5	19	•
ARPG93-11	M	27	5	1993		•	33.0	96.0	82.0	5.0	18	•
ARPG93-12	F	1	6	1993	9	9.170	55.0	120.0	98.0	5.0	30	•
ARPG93-13	F	1	6	1993	0	0.170	21.0	87.0	71.0	3.5	10	•
ARPG93-14	F	1	6	1993	1	1.170	26.0	93.0	75.0	3.5	13	
ARPG93-15	M	1	6	1993	3	3.170	35.0	109.0	89.0	3.0	18	•
ARPG93-16	F	3	6	1993	7	7.175	48.0	122.0	86.0	3.5	24	
ARPG93-17	F	3	6	1993	5	5.175	59.0	125.0	104.0	4.0	31	•
ARPG93-18	F	3	6	1993	0	0.175	27.0	93.0	78.0	4.9	19	
ARPG93-19	М	10	7	1993	6	6.277	35.0	109.0	77.0	3.5	15	
ARPG93-20	F	13	7	1993	5	5.277	35.0	106.0	78.0	2.5	16	
ARPG93-21	M	13	7	1993	16	16.277	43.0	119.0	88.0	3.0	20	
ARPG93-22	F	13	7	1993	2	2,277	42.0	115.0	85.0	3.0	23	
ARPG93-23	М	14	7	1993	9	9,279	65.0	127.0	103.0	5.0	31	
ARPG93-24	M	14	7	1993	5	5.279	40.0	126.0	90.0	4.0	19	
ARPG93-25	М	14	7	1993	4	4.279	44.0	124.0	94.0	4.4	21	
ARPG93-26	M	14	7	1993	2	2.279	41.0	118.0	86.0	4.0	20	•
ARPG93-27	F	14	7	1993	•	•	39.0	117.0	75.0	3.0	18	
ARPG93-28	М	14	7	1993	2	2.279	29.0	98.0	71.0	3.0	14	
ARPG93-29	F	14	7	1993	1	1.279	36.0	110.0	79.0	2.5	16	•
ARPG93-30	M	14	7	1993	3	3.279	34.0	113.0	73.0	2.5	15	
ARPG93-41	М	31	8	1993	1	1.419	22.0	81.0	69.0	3.5	11	
ARPG93-42	F	21	9	1993	1	1.499	16.0	92.0	66.0	3.0	9	
ARPG93-43	M	21	9	1993	0	0.499	30.0	100.0	73.0	4.0	12	•
ARPG93-44	F	21	9	1993	0	0.499	20.0	89.0	68.0	4.0	10	
ARPG93-45	M	21	9	1993	0	0.499	25.0	97.0	70.0	2.5	10	
ARPG93-46	M	21	9	1993	1	1.499	40.0	112.0	83.0	4.5	19	
ARPG93-47	F	21	9	1993	0	0.499	25.0	93.0	66.0	3.0	9	•
ARPG93-48	М	23	9	1993	0	0,505	24.0	89.0	72.0	3,2	11	•
ARPG93-49	М	29	9	1993	0	0.521	32,0	100.0	76,0	4.5	19	•
ARPG93-50	F	30	9	1993	14	14.523	57.0	119.0	100.0	5.5	22	•

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ARPG95-14	F	16	1	1996	2	2.797	31.0	108.0	85.0	4.0	15	
ARPG95-15	М	16	1	1996	5	5.797	41.0	112.0	90.0	5.0	19	•
ARPG95-16	F	31	1	1996	21	21.838	65.0	120.0	106.0	5.0	33	
ARPG95-17	M	31	1	1996	4	4.838	35.0	108.0	82.0	4.0	17	•
ARPG95-18	F	31	1	1996	7	7.838	60.0	120.0	100.0	6.0	31	
ARPG95-19	M	31	1	1996	3	3.838	41.0	111.0	87.0	4.5	17.5	
ARPG95-20	M	31	1	1996	3	3.838	33.0	109.0	80.0	4.0	15	•
ARPG95-21	M	11	2	1996	21	21.868	50.0	133.0	118.0	6.0	40	
ARPG95-22	M	13	2	1996	6	6.874	53.0	123.0	102.0	4.0	34	•
ARPG95-23	M	15	2	1996	8	8.879	85.0	144.0	48.0	5.0	40	
ARPG95-24	M	16	2	1996	5	5.882	55.0	112.0	98.0	4.0	25	•
ARPG95-25	M	16	2	1996	5	5.882	75.0	127.0	112.0	5.0	31	•
ARPG95-26	F	16	2	1996	8	8,882	60.0	119.0	100.0	4.5	37	
ARPG95-36	M		2	1996	8	8.882	56,0	125.0	95.0	4.5	34	
ARPG95-37	F		2	1996	2	2.882	38.0	100.0	89.0	3.5	21	
ARPG95-38	M	27	2	1996	4	4.912	43.0	108.0	91.0	5.0	21	
ARPG95-39	M	27	2	1996	12	12.912	55.0	116.0	109.0	4.5	32	
ARPG95-40	M	29	2	1996	3	3.918	40.0	107.0	95,0	4.0	18	•
ARPG95-41	F	29	2	1996	6	6.918	39.0	107.0	92.0	4.5	19	
ARPG95-42	F	4	3	1996	5	5.929	49.0	107.0	92.0	4.0	•	•
ARPG95-43	M	5	3	1996	7	7.932	41.0	112.0	89.0	4.5	19	
ARPG95-44	M	5	3	1996	7	7.932	40.0	110.0	93.0	5.5	15	•
ARPG95-45	F	5	3	1996	6	6.932	55.0	124.0	100.0	5.0	24	•
ARPG95-46	М	5	3	1996	6	6.932	46.0	119.0	95.0	4.5	22	•
ARPG95-47	M	7	3	1996	0	0.937	21.0	84.0	74.0	4.0	9	•
ARPG95-48	M	7	3	1996	3	3,937	28.0	96.0	80.0	4.5	12	•
ARPG95-49	M	8	3	1996	3	3.940	41.0	116.0	90.0	4.5	19	•
ARPG95-50	M	8	3	1996	1	1.940	25.0	94.0	75.0	3.5	12	•
ARPG95-51	M	14	3	1996	2	2.956	31.0	93.0	81.0	4.0	12	•
ARPG95-52	M	15	3	1996	1	1.959	28.0	95.0	75.0	3,5	10	•
ARPG95-53	M	17	3	1996	15	15.964	73.0	113.0	110.0	4.5	30	•
ARPG95-54	M	17	3	1996	1	1.000	25.0	91.0	78.0	3.0	11	•

ARPG95-55	F	19	3	1996	5	5.970	49.0	116.0	100.0	6.0	21	
ARPG95-56	M	19	3	1996	5	5.970	44.0	114.0	94.0	4.0	19	•
ARPG95-57	M	23	3	1996	23	23.981	66.0	130.0	110.0	4.0	31	
ARPG95-58	F	28	3	1996	4	4.995	41.0	114.0	90.0	4.0	20	
ARPG95-59	M	28	3	1996	1	1.995	25.0	98.0	78.0	3.0	10	
ARPG95-60	F	28	3	1996	4	4.995	40.0	110.0	91.0	3.0	20	•
ARPG95-61	M	28	3	1996	2	2.995	28.0	110.4	86.0	6.0	15	•
ARPG95-62	F	28	3	1996	6	6.995	36.0	107.0	88.0	4.0	19	•
ARPG95-63	F	28	3	1996	4	4.995	47.0	120.0	86.0	5.0	20	
ARPG95-64	M	28	3	1996	7	7.995	70.0	136.0	114.0	5.5	32	
ARPG95-65	F	31	3	1996	3	3.000	34.0	98.0	86.0	3.0	11	
ARPG95-66	F	31	3	1996	5	5.000	41.0	110.0	91.0	4.0	19	•
ARPG95-67	F	31	3	1996	5	5,000	49.0	111.0	103,0	4.5	20	•
ARPG95-68	F	28	4	1996	18	18.077	62.0	124.0	103,0	6.0	30	•
ARPG95-69	M	29	4	1996	14	14.079	49.0	123.0	92.0	4.5	27	•
ARPG95-70	M	10	5	1996	11	11.110	75.0	134.0	114.0	6.0	34	•
ARPG95-71	F	25	5	1996	6	6.151	40.0	105.0	89.0	4.0	17	•
ARPG95-72	M	25	5	1996	38	38,151	47.0	137.0	85,0	2.5	16	•
ARPG95-73	M	25	5	1996	4	4.151	38.0	112.0	84.0	4.5	17	•
ARPG95-74	M	25	5	1996	21	21.151	56.0	133.0	96.0	4.0	20	•
ARPG95-75	F	25	5	1996	5	5.151	43.0	116.0	90.0	4.5	22	•
ARPG95-76	M	25	5	1996	11	11.151	51.0	125.0	85.5	3.5	23	•
ARPG95-77	F	25	5	1996	2	2.151	27.0	110.0	83.0	4.0	13	•
ARPG95-78	M	7	6	1996	24	24.186	57.0	132.0	96.0	3.0	22	•
ARPG95-79	М	14	6	1996	5	5.205	25.0	103.0	73.0	3.0	10	•
ARPG95-80	F	14	6	1996	1	1.205	30.0	101.0	80.0	4.0	17	•
ARPG95-81	М	16	6	1996	9	9.211	56.0	127.0	86.0	4.0	23	•
ARPG95-82	F	1	7	1996	7	7.252	39.0	115.0	77.0	3.0	•	17
ARPG95-83	M	1	7	1996	6	6.252	32.0	113.0	70.0	3.5	•	13
ARPG95-84	F	1	7	1996	7	7.252	29.0	100.0	69.0	2.0	•	10
ARPG95-85	M	1	7	1996	1	1.252	23.0	88.0	64.0	4.0	•	8
ARPG95-86	F	1	7	1996	2	2.252	27.0	104.0	70.0	4.0	•	12

ARPG95-87	F	1	7	1996	1	1.252	23.0	93.0	69.0	4.5	•	13
ARPG95-88	F	3	7	1996	10	10.258	35.0	125.0	75.0	3.5	•	12
ARPG95-89	M	2	7	1996	0	0.255	22.0	90.0	63,0	3.5	•	10
ARPG95-90	М	5	7	1996	0	0.263	19.0	90.0	61.0	3,5	•	7
ARPG95-91	F	6	7	1996	0	0.266	18.0	90.0	63.0	3,0	•	9
ARPG95-92	F	8	7	1996	8	8,271	47.0	113.0	80,0	5.0	•	19
ARPG95-93	F	8	7	1996	14	14.271	49.0	119.0	76.0	4.0	•	20
ARPG95-94	F	8	7	1996	1	1,271	20.0	89.0	61.0	4.0	•	9
ARPG95-95	F	9	7	1996	2	2.274	27.0	100.0	71.0	3.0	•	11
ARPG95-96	M	9	7	1996	4	4.274	34.0	110.0	70.0	3,0	•	15
ARPG95-97	M	9	7	1996	5	5.274	36.0	118.0	78.0	3.0		•
ARPG95-98	M	9	7.	1996	12	12.274	55.0	132.0	90.0	4.0		21
ARPG95-99	M	10	7	1996	8	8.277	45.0	125.0	79.0	2.5		17
ARPG95-100	M	10	7	1996	2	2.277	32.0	104.0	82.0	4.5	•	15