MASS DYNAMICS OF WEDDELL SEALS

IN EREBUS BAY, ANTARCTICA

by

Kelly Michelle Proffitt

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

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in

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ABSTRACT

An individual's body mass is an important life history trait that may vary with environmental conditions and be related to reproductive performance. In this dissertation, we used a 35-year dataset to investigate variations in body mass of Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica with goals of linking environmental conditions, body mass, and reproductive performance. We predicted that variations in environmental conditions and maternal traits would correlate with variations in maternal body mass at parturition, and that variations in maternal body mass may be linked with offspring's body mass and survival probability. We found maternal body mass at parturition showed substantial age- and environmental-related variations. Maternal body mass increased with age through the young and middle ages, and evidence of senescent declines in body mass was found amongst the oldest ages. Additionally, body mass at parturition was strongly influenced by environmental variations during the pregnancy period, specifically body mass was negatively correlated with sea-ice extent and positively correlated with the Southern Oscillation. Annually, pup weaning mass was highly variable. Pup weaning mass was negatively correlated with summer sea-ice extent and positively correlated with summer Southern Oscillation, and these two variables explained 86% of the annual variation in the population average weaning mass. Weaning mass was positively correlated with juvenile survival probability, particularly for males, and we estimated the odds of a male surviving from weaning to age 3 increased 7.3% for every 10 additional kilograms of body mass accrued by weaning. Together, these results suggest large-scale atmospheric-oceanographic variations may affect Weddell seal maternal foraging success and ultimately reproductive performance. Finally, we investigated statistical methodologies accounting for measurement error in photogrammetrically estimated body mass with goals of developing techniques to employ estimated body mass as a covariate in simple linear regression models. We demonstrated that error associated with estimating body mass induces bias in regression statistics and decreases model explanatory power and we described simple statistical techniques accounting for measurement error in covariates. These statistical developments may allow future studies to employ photogrammetric mass estimation techniques and utilize estimated body mass as a covariate in ecological modeling exercises.

CHAPTER 1

INTRODUCTION TO DISSERTATION

Introduction

The Weddell seal (*Leptonychotes weddellii*) population in Erebus Bay, Antarctica is one of the world's most studied marine mammal populations (Cameron and Siniff 2004, Figure 1.1).

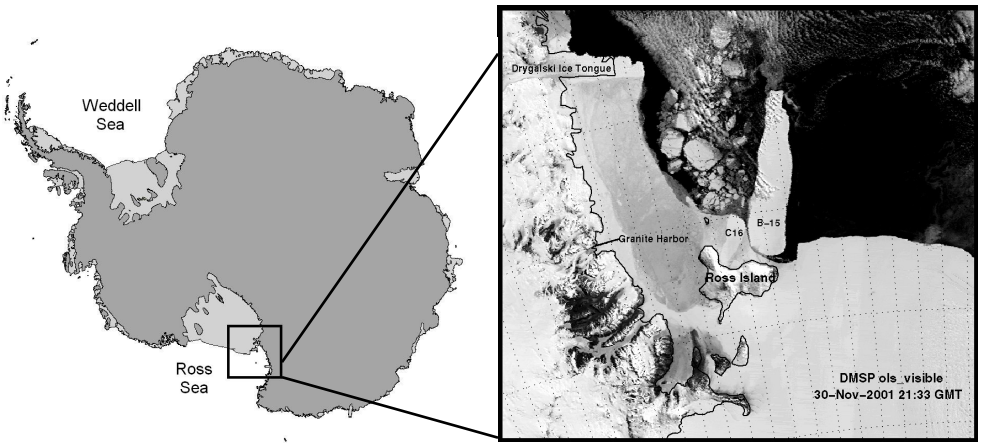


Figure 1.1 The Erebus Bay study area is located in the southeastern corner of McMurdo Sound (right panel), in the western Ross Sea, Antarctica (left panel).

Each austral spring, 8 to 14 pupping colonies form in Erebus Bay along perennial cracks in the sea ice and females use these cracks to access the fast ice surface for pupping. Following pupping, females remain in close association with their pups during the lactation period (Stirling 1969, Tedman and Bryden 1979) and spend the majority of their time on the fast ice surface where they are easily approachable and accessible to researchers. Males and non-pupping females also aggregate in these colonies for breeding which occurs during the later portion of the lactation period. Accessibility of

animals on the fast ice near breeding colonies, combined with strong philopatry to the Erebus Bay population (Cameron *et al.* 2007), make the Weddell seal an ideal animal for studying the population dynamics and life history traits of a long-lived mammal.

Long-term monitoring of individual Weddell seals in Erebus Bay has resulted in a comprehensive mark-resighting database, allowing researchers to employ sophisticated population modeling techniques to learn about the dynamics of long-lived animal populations and the life history traits of individual animals. Recent studies have estimated the extent of within-population variation in important life-history characteristics, and found remarkable heterogeneity in individual maternal quality and reproductive performance (Hadley 2006). Additionally, these studies identified potential linkages between reproductive performance, as measured by offspring survival probability, and environmental variations (Hadley *et al.* 2007). However, the mechanisms responsible for variations in life history traits or those that link variations in environmental conditions and reproductive performance are not well understood. In this dissertation, we investigate variations in body mass with goals of identifying relationships between environmental variations, body mass, and reproductive performance.

An individual's body mass is an important attribute that may be linked with variations in life history traits and reproductive performance (Roff 1992). Body mass may determine when an animal begins reproduction (Reiter and LeBoeuf 1991, Saether and Heim 1993), the amount of energy allocated to offspring (Arnbom et al. 1997), and ultimately offspring survival probability and maternal fitness. However, in spite of the importance of maternal body mass in affecting patterns of energy expenditure during

reproduction (Arnbom *et al.* 1997, Wheatley *et al.* 2006), offspring size at weaning (Bowen *et al.* 2001, Crocker *et al.* 2001), and offspring survival probability (Hall *et al.* 2001, McMahon and Burton 2005), little is known about sources of variation in this important life history trait (Schultz and Bowen 2004). Previous studies have documented positive relationships between body mass and age, however much of the variation in body mass is not explained by maternal age, and relationships between body mass and environmental conditions and maternal traits such as reproductive experience or age at maturity are largely unexplored.

The objective of this dissertation research was to explore sources of variation in Weddell seal body mass with goals of 1) relating variations in body mass to large-scale atmospheric oceanographic conditions, 2) relating variations in body mass to maternal traits, and 3) relating variations in pup body mass with juvenile survival probability. In Chapter 2, we investigated relationships between maternal body mass at parturition and maternal traits (age, reproductive experience, and age at maturity) and large-scale atmospheric oceanographic variations (sea-ice extent and Southern Oscillation). Environmental variations may have profound effects on the biotic components of marine ecosystems (Walther *et al.* 2002), and these variations may affect seal foraging success and body mass. Further, body mass may vary with age, reproductive experience, or individual quality, and we hypothesized that age-specific variations in body mass may be similar to the recently documented patterns of age-specific reproductive performance (Hadley *et al.* 2007).

Chapter 3 further explored linkages between large-scale atmospheric oceanographic variations and annual pup weaning masses. Using data collected over 31-

years, relationships between environmental variability and annual average pup weaning masses were evaluated. Weaning masses represent the foraging success of pregnant seals, a trait that may vary annually in response to environmental conditions and variability in the Ross Sea food web. Chapter 4 explored relationships between body mass at weaning and juvenile survival probabilities, and we hypothesized that animals with higher body mass at weaning would have higher juvenile survival rates. We estimated age- and sex-specific survival rates, and investigated potential relationships between body mass at weaning and juvenile survival rate (survival from weaning to age 3).

Although body mass is an important life history trait, the body mass of large mammals may be a difficult trait to directly measure in the field. Photogrammetric mass-estimation techniques have been developed to indirectly estimate the body mass of several species of large phocids (Haley *et al.* 1991, Bell *et al.* 1997, Ireland *et al.* 2006), and these techniques provide a safe and efficient methodology for collecting body mass estimates. However, when a photogrammetrically estimated mass is used as a covariate in regression modeling, the prediction error associated with estimating body mass induces bias in regression statistics and decreases model explanatory power. Thus, it is important to understand and account for prediction variance when addressing ecological questions that require use of estimated mass values. Chapter 5 explores prediction variance in photogrammetrically estimated masses and provides techniques for accounting for prediction in biological analyses. Chapter 6 provides a synthesis of these findings and suggests directions for future mass dynamics research.

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CHAPTER 2

ENVIRONMENTAL AND SENESCENT RELATED VARIATIONS IN WEDDELL SEAL BODY MASS: IMPLICATIONS FOR AGE-SPECIFIC REPRODUCTIVE PERFORMANCE

Abstract

Recent studies have found age-specific variations in reproductive performance amongst Weddell seals (*Leptonychotes weddellii*), and we hypothesized age-related variations in maternal body mass as a mechanism linking maternal age and the observed patterns of reproductive performance. We evaluated the effects of maternal traits such as age and reproductive experience and the effects of environmental variations on maternal body mass at parturition. Maternal body mass at parturition showed substantial age- and environmental-related variations. Maternal body mass increased with age through the young and middle ages, and evidence of senescent declines in body mass was found amongst the oldest ages. Additionally, body mass at parturition was strongly influenced by environmental variations during the pregnancy period, specifically sea-ice extent and the state of the El-Niño Southern Oscillation. Patterns of age-specific variations in body mass were consistent with age-specific patterns of offspring survival probability, which supported our hypothesis that changes in body mass link maternal age and reproductive performance in the Weddell seal. Further, environmental conditions during pregnancy may be an important component of Weddell seal reproductive performance.

Introduction

Life history theory predicts that an individual's reproductive performance should change with age because of age-related changes in the trade-off between present offspring and future reproduction and the optimal reproductive effort. Age-related variations in reproductive performance are observed across a range of taxa including birds (Nol and Smith 1987, Weimerskirch 1992, Saether 1990, Robertson and Rendell 2001), ungulates (Clutton-Brock 1988, Mysterud *et al.* 2001), and marine mammals (Lunn *et al.* 1994, Bowen *et al.* 2006), and several hypotheses have been proposed to explain improved reproductive performance with age. "Restraint" hypotheses predict that animals will withhold reproductive effort early in their lives because residual reproductive value is high, whereas "constraint" hypotheses explain increases in reproductive performance with age based on age-related improvements in individual competence (Curio 1983, Saether 1990, Nol and Smith 1987). Additionally, decreased reproductive performance amongst the oldest age classes is predicted by life history theory (Hamilton 1966, Williams 1975, Abrams 1991), and evidence of senescent declines in reproductive performance has been well documented (Weimerskirch 1992, Packer *et al.* 1998, Robertson and Rendell 2001, Bowen *et al.* 2006).

Long-term studies on Weddell seals (*Leptonychotes weddellii*) have found remarkable heterogeneity in age-specific life history traits (Hadley 2006), including age-specific variation in offspring survival probability (Hadley *et al.* 2007). Offspring survival probability was positively related to maternal age, however, this relationship was not uniform across all the reproductive age classes in this long-lived species. The

increases in offspring survival probability declined as maternal age increased, and there were only minimal increases to offspring survival probability after mothers reached middle age. Although complex patterns of age-related variation in reproductive performance are documented (Saether 1990, Weimerskirsch 1992, Bowen *et al.* 2006), the mechanisms through which age exerts its influence are not well understood.

In capital breeding species, body mass may affect reproductive performance, (Chastel *et al.* 1995, Arnbom *et al.* 1997, Festa-Bianchet *et al.* 1998, Bowen *et al.* 2001), and we hypothesized that age-related variations in maternal body size might be a mechanism linking maternal age and the observed patterns of Weddell seal reproductive performance (Hadley *et al.* 2007). In phocid seals, older females are expected to have higher body mass than younger females when they give birth (Hill 1987, Crocker *et al.* 2001). Females do not regularly feed during lactation and support the costs of lactation and pup rearing primarily through the mobilization of stored energy reserves (Boness and Bowen 1996). Therefore, females with higher body mass at parturition are expected to transfer more energy to offspring during lactation (Wheatley *et al.* 2006) and to thereby wean pups of higher body mass than their counterparts with lower body mass at parturition (Hill 1987). Higher body mass at weaning may confer a survival advantage to pups (Baker and Fowler 1992, McMahon *et al.* 2000), and therefore, variations in maternal body mass (which affects offspring weaning mass) may explain relationships between maternal age and offspring survival.

Senescent declines in multiple measures of female reproductive performance have been documented amongst long-lived species (Weimerskirch 1992, Packer *et al.* 1998, Bowen *et al.* 2006), and in some species, senescent declines in female body mass

preceded declines in reproduction (Bérube *et al.* 1999). The nonlinear relationship between Weddell seal maternal age and offspring survival probability and lack of a substantial increase in survival probability of offspring born to the oldest mothers may reflect senescent declines in reproductive performance (Hadley *et al.* 2007). In accordance with our prediction that body mass may be a mechanism linking maternal age and reproductive performance, we hypothesized that Weddell seals may experience senescent related declines in body mass. In the oldest age classes, this may explain the observed patterns of reproductive performance.

Our goals in this paper were to investigate sources of variation in Weddell seal maternal body mass at parturition, and to relate age-specific variations in body mass with patterns of reproductive performance. In spite of the importance of body mass in potentially affecting female post-partum reproductive performance (Arnbom *et al.* 1997, Festa-Bianchet *et al.* 1998), maternal characteristics (such as age or experience) and environmental variations affecting this important life history trait are not well understood (Schultz and Bowen 2004). We hypothesized that variation in maternal body mass at parturition was related to maternal traits such as age, reproductive experience, and age at primiparity, as well as variations in environmental conditions such as sea-ice extent and El-Niño Southern Oscillation (ENSO). We predicted that maternal mass would increase through the young and middle age classes and then decline in the oldest age classes. Additionally, we predicted that mothers with younger age at primiparity (i.e. higher quality individuals, Hadley 2006) may be either superior foragers or genetically predisposed to larger body size and would therefore, have higher body mass at a given age than their counterparts who delayed primiparity. Finally, we hypothesized that

mothers with higher reproductive experience may be superior quality females, and may also have higher body mass than their counterparts with less reproductive experience.

Our age-related hypotheses represent consistent and predictable mechanisms believed to be operating on variations in maternal parturition mass. However, stochastic processes are also expected to influence body mass (LeBoeuf and Crocker 2005, Hadley *et al.* 2007, Proffitt *et al.* 2007). To gauge the relative contribution of predictable and stochastic influences on maternal body mass, we evaluated relationships between large-scale atmospheric-oceanographic variations and maternal body mass at parturition. Sea-ice extent shows large intra- and inter-annual variations, and is correlated with variations in the distribution and abundance of phytoplankton, Antarctic krill and top predators (Loeb *et al.* 1997, Nicol *et al.* 2000, Barbraud and Weimerskirch 2001a). Summer sea-ice extent determines the extent of open-water primary production and therefore, may influence zooplankton and fish abundance and consequently, food resources available to pregnant seals. We hypothesized that decreased summer sea-ice extent (i.e. increased open water extent) may increase food resources available to pregnant seals, resulting in higher parturition masses the following pupping season. In addition, Antarctic sea-ice and Southern Ocean ecosystems are affected by large scale ocean-atmospheric variations associated with the ENSO signal that produce changes in sea-surface temperatures and sea-ice conditions (Ledley and Huang 1997, Kwok and Comiso 2002). We predicted that positive phases of the Southern Oscillation may create favorable foraging conditions and result in higher parturition masses (Proffitt *et al.* 2007).

Methods

Study System

The study population of Weddell seals reported on here occupies Erebus Bay, located in the western Ross Sea, Antarctica (77°44'S, 166°30'E, see Cameron and Siniff 2004 for detailed description of the study area). Each austral spring, 8 to 14 pupping colonies form along perennial cracks in the sea ice created by tidal movement of the fast ice against land or glacial ice. Pupping occurs on the fast ice surface from late October to November, and mothers remain in close association with their pups throughout the 30-50 day lactation period (Stirling 1969, Tedman and Bryden 1979, Wheatley *et al.* 2006). Females come into estrous approximately 35 days after parturition, and polygynous breeding occurs in underwater territories centered on the ice cracks at each colony (Hill 1987, Gelatt *et al.* 2000). Females are iteroparous breeders, generally reaching sexual maturity at about 7 years of age (Hadley *et al.* 2006). The oldest known breeding female in this population was 28 years old, although animals in the oldest age classes are rare (unpublished data).

From 1969 to present, pups born within the Erebus Bay study area have been marked with individually numbered tags (Siniff *et al.* 1977), and since 1973, multiple annual mark-resight surveys of the seal population have been conducted. At the time of tagging and during each resighting event, the date, location, tag number, relative's tag numbers (if any) have been recorded and added to the long-term database. Most females surviving to reproductive age return to breed in Erebus Bay and individual resighting rates are high (Cameron and Siniff 2004). Reproductive-aged males and females

demonstrate strong philopatry to the Erebus Bay breeding colonies (Cameron *et al.* 2007) and long-term individual surveys and high resightability have resulted in comprehensive resighting histories for each marked animal.

Body Mass Measurements

Maternal body mass at parturition was measured from 2002 to 2005. Pupping colonies were surveyed approximately every 24-48 hours. In 2002-2003 females were randomly selected for sampling, and in 2004-2005, animals were randomly selected for sampling from within each of three maternal age classes (<8, 8-16, 17+ years old). We strived to measure body mass 24-72 hrs post-parturition. Mass was measured using one of two methods: suspending animals from a spring scale (2002-2003) or coercing animals onto a digital weighing platform (Maxey Manufacturing, Fort Collins, CO, 2004-2005). Both methodologies accurately estimated body mass to within 0.5kg, and the timing of parturition mass measurements was consistent among years. Although parturition masses were measured at different colonies among and within years, our previous analyses do not indicate inter-colony variation in maternal parturition mass (this study, unpublished data).

Model Covariates

Three covariates representing maternal traits potentially affecting maternal parturition mass were derived from the long-term database and evaluated: age (Age), reproductive experience (Exp), and age at primiparity (AgeFirst). Age was measured as years since the animal was marked as a pup. Maternal experience was defined as the number of pups that an individual had produced. Age at primiparity was the age at which

an individual's first pup was produced. Four environmental covariates potentially influencing maternal parturition mass were also evaluated: summer sea-ice extent (SumExtent), winter sea-ice extent (WinExtent), summer Southern Oscillation (SumSOI), and winter Southern Oscillation (WinSOI). Sea-ice extent was measured over the Ross Sea sector of Antarctica from passive microwave satellite images (DMSP SSM/I) (Comiso 1999). Winter maximum sea-ice extent was defined as the September average and summer minimum sea-ice extent was defined as the February average. The strength of the El-Niño Southern Oscillation was measured by the Southern Oscillation index and calculated as the three month running average over summer (Dec-Feb) and winter (July-Sept, Bureau of Meteorology 2006).

Model Development and Evaluation

We used a linear modeling approach to evaluate competing hypotheses regarding variations in maternal body mass (R Development Core Team 2005). Maternal age, experience, and age at first parturition and the environmental variables were all continuous covariates treated as fixed effects. We considered both maternal identity and year as random effects but did not have adequate numbers of females or years with repeated samples to legitimately analyze them as such. Therefore, we treated year as a fixed effect and did not evaluate maternal identity.

We evaluated two potential functional forms of the relationship between maternal parturition mass and age: quadratic and asymptotic, represented by Age(quad) and Age(asy), respectively (Franklin *et al.* 2000). The quadratic form predicted an optimal minimum or maximum response at intermediate values of the covariate, with lesser

effects at the extremes, and was expressed as $\beta_i x_i + \beta_{i+1} x_i^2$. The asymptotic form predicted the response approached but never reached an asymptote as x_i increased, and was expressed as $\beta_i \ln(x_i)$. Each functional form corresponded to a biologically plausible relationship between maternal parturition mass and age. In the quadratic model, body mass increased through the younger ages, reached a maximum at prime age, and then decreased amongst the oldest age classes. In the asymptotic model body mass increased in the younger ages, then leveled off as age increased. Age in the quadratic form represented the hypothesis of senescent declines in maternal body mass, and age in the asymptotic form represented the hypothesis that maternal body mass leveled off, but did not decline, in the oldest age classes. In the *a priori* model set, we considered only linear forms of the other covariates because hypothesized relationships for each of these covariates were linear.

Hypotheses representing the relationships between the response variable (maternal body mass) and model covariates were developed and expressed as a set of competing models. We considered nineteen models explaining variation in maternal parturition mass using various combinations of maternal and environmental covariates. Variance inflation factors (VIF), which measure the degree of multi-collinearity among variables, were calculated for all combinations of predictors. Those models that included predictor combinations with VIF>5 were removed from the list of competing models (Neter *et al.* 1996). A total of 30 models were evaluated (11 of the 19 model forms were evaluated using two functional forms of the covariate age).

We used Akaike's Information Criterion corrected for sample size, AIC_c, and Akaike model weights (w_i) to quantify the support from the data for each of our hypothesized models and to address model-selection uncertainty (Burnham and Anderson 2002). To assess the relative importance of each predictor variable, we calculated a predictor weight for each of the *R* predictors, $w_{+(j)}$, by summing Akaike weights for all *a priori* models containing predictor x_j, for $j = 1, \ldots, R$ (Burnham and Anderson 2002). Model-averaged coefficient and variance estimates for each covariate (of a given functional form) were computed across all models (Burnham and Anderson 2002).

Results

A total of 92 parturition masses were collected from 86 different females from 2002-2005 (6 animals were sampled in two different years). Mean maternal body mass was 432.0 ± 50.4 kg (range 278.2-539.0, Table 1). Mean maternal age was 13.0 ± 4.5 years (range 6-22, cv = 0.35), mean reproductive experience was 5.0 ± 3.2 pups produced (range 1-15, cv = 0.64), and mean age at first parturition was 7.2 ± 1.5 years (range 4-12, cv = 0.21). Although only four years of data were collected, a wide range of environmental conditions were captured. Mean summer sea-ice extent was 8.5 ± 2.5 $x10^6 km^2$ (cv = 0.29), winter sea-ice extent was 39.0 ± 2.3 $x10^6 km^2$ (cv = 0.06), summer southern oscillation index was -3.4 ± 5.7 (cv = 0.65), and winter southern oscillation was -4.2 ± 3.7 (cv = 0.65).

Table 2.1 Summary statistics for maternal body mass at parturition of Weddell seals in Erebus Bay, Antarctica. Annual mean, minimum (Min), maximum (Max), standard deviation (SD) and sample sizes (*n*) are presented along with the overall values calculated across all observations.

Year	*Mean (kg)*	*Min (kg)*	*Max (kg)*	*SD (kg)*	*n*
2002	437.6	395.0	483.0	31.5	19
2003	399.0	278.2	474.0	53.0	21
2004	437.0	338.0	539.0	47.7	31
2005	456.3	360.5	529.5	51.1	21
Overall	432.8	278.2	539.0	50.4	92

We found substantial support for our hypothesis that both maternal age and environmental variations influenced maternal body mass at parturition, and we found evidence of senescent declines in body mass. The top ranked model included the covariates maternal age (quadratic form), summer sea-ice extent, and summer southern oscillation, and these covariates together explained 49% of the variation in maternal parturition mass ($w_k = 0.43$, Table 2).

Table 2.2 Model selection results for *a priori* models examining the effects of covariates on variation in Weddell seal maternal parturition mass. Covariates included maternal age quadratic (Age(quad)) and asymptotic (Age(asy)) forms, reproductive experience (Exp), age at primiparity (AgeFirst), summer sea-ice extent (SumExtent), winter sea-ice extent (WinExtent), and summer southern oscillation (SumSOI). The top 10 *a priori* models are presented along with the number of parameters (K), the ΔAIC_c value, and the Akaike weight (w_k). The AIC_c score of the top model was 933.1.

Model List	*K*	ΔAIC_c	w_k
Age(quad)+ SumExtent + SumSOI	6	0.00	0.43
Age(quad)+ SumExtent + WinExtent	6	2.11	0.15
Age(quad)+ Exp + SumExtent + SumSOI	7	2.28	0.14
Age(asy) + SumExtent + SumSOI	5	3.95	0.06
Age(quad)+ Exp + SumExtent + WinExtent	7	4.32	0.05
Age(quad)+ AgeFirst + Exp + SumExtent + SumSOI	8	4.68	0.04
Age(quad)+ SumExtent	5	5.46	0.03
Age(asy) + Exp + SumExtent + SumSOI	6	5.52	0.03
Age(quad)+ AgeFirst + Exp + SumExtent + SumSOI + WinExtent	9	5.84	0.02
Age(asy) + SumExtent + WinExtent	5	6.25	0.02

The relationship between age and parturition mass was best characterized by the quadratic form, indicating that parturition mass was lower at the youngest and oldest age classes, and highest at the middle age classes ($\hat{\hat{\beta}}_{Age} = 26.0$, 95% CI = [6.9, 45.1], $\hat{\hat{\beta}}_{Age^2} = -0.72$, 95% CI = [-1.13, -0.31]). Body mass increased with maternal age until reaching a maximum at age 18, and then declined throughout the oldest ages (Figure 1). Using the top model structure, and holding other coefficients at their mean, predicted body mass for a young mother (age 6) was 363.7 kg (CI = [310.1, 417.3]), a prime-aged mother (age 18) was 465.1 kg (CI = [391.3, 538.9]), and a senescent mother (age 25) was 429.9 kg (CI = [397.9, 462.0]). Relative to the other maternal traits which we evaluated, Age(quad) was the strongest predictor of maternal body mass ($w_{+(j)} = 0.86$). We did not

find support for our hypothesis that experienced mothers had higher body mass than their inexperienced counterparts ($w_{+(j)} = 0.10$). Additionally, there was little support for the hypothesis that animals first reproducing at younger ages had a higher body mass given their current age ($w_{+(j)} = 0.06$).

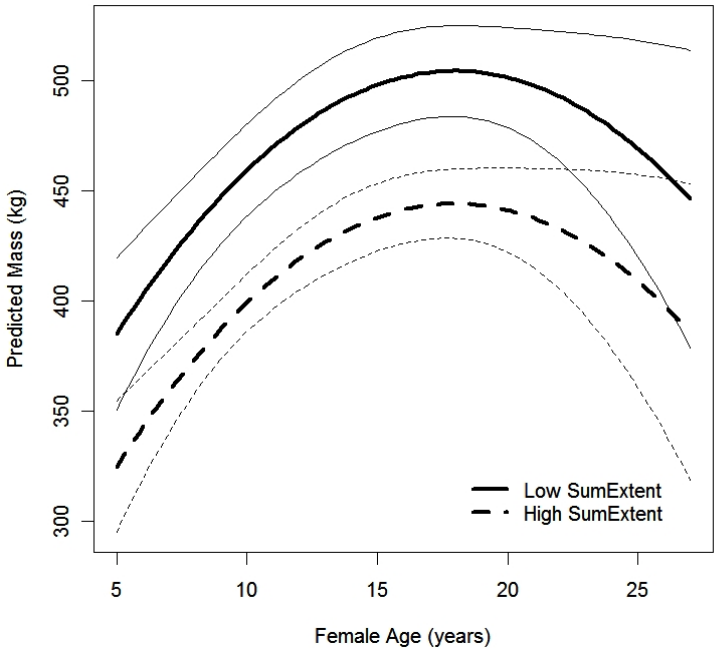


Figure 2.1 The predicted mean parturition mass (bold lines) and 95% confidence intervals (thin lines) for Weddell seal mothers of varying ages following summers of low (solid lines) and high sea-ice extent (dashed lines).

We found strong support for our hypotheses that environmental variations affected pregnant animals' ability to accumulate body mass to fuel the energetic costs of lactation. Maternal body mass was higher following summers with low sea-ice extent and positive phases of the southern oscillation ($\hat{\bar{\beta}}_{SumExtent} = -6.72$, 95% CI = [-13.68, 0.25], $\hat{\bar{\beta}}_{SumSOI} = 2.44$, 95% CI = [0.65, 4.23]). Model-averaged coefficients estimated

maternal body mass varied from 486.6 kg (95% CI = [469.4, 503.8]), to 447.7 kg (95% CI = [412.9, 482.4]), to 426.5 kg (95% CI = [382.2, 470.9]), between years of low, average, and high summer sea-ice extent (estimates created from the minimum, average, and maximum values observed during this study, using the top model structure, and holding other coefficients at their mean). Relative to the other predictors that we evaluated, SumExtent was the best environmental predictor and the best overall predictor of maternal parturition mass ($w_{+(j)} = 0.99$). Stochastic effects produced variations in body mass that were as strong as age-related effects (Figure 1). Following a summer of high sea-ice extent, a prime-aged female (age 18) was predicted to accrue body mass roughly equal to an eight year old female following a summer with low sea-ice extent.

Discussion

The patterns of age-specific variations in body mass found in this study are consistent with patterns of offspring survival probability, and support our hypothesis that body mass may be a mechanism linking maternal age and reproductive performance. Body mass initially increased with age, reached a maximum at intermediate age, and then showed senescent declines at the oldest ages. Additionally, we found that body mass was strongly affected by environmental variations, suggesting that large scale atmospheric oceanographic variations may affect Weddell seal foraging success and ultimately reproductive performance. These results have important consequences for age-specific reproductive performance, as well as implications for reproductive success in a changing climate.

Weddell seal offspring survival rate has been shown to initially increase with maternal age, until reaching a plateau in the middle ages after which further increases in maternal age confer little advantage (Hadley *et al.* 2007). Here, we found that Weddell seal body mass increased rapidly during the younger ages, slowly continued to increase to a maximum in the middle ages, and declined amongst the oldest ages. Increases in body mass over the younger age classes likely result in increasing energy transfer to offspring (Wheatley *et al.* 2006) and may confer a survival advantage to pups during the post-weaning fast (Baker and Fowler 1992, McMahon *et al.* 2000). The declining rate of increase in body mass by middle age may result in the pattern of decreasing influence of maternal age on offspring survival found in Hadley *et al.* (2007). Patterns of age-specific variation in body mass and offspring survival amongst the oldest age classes are disparate; body mass is predicted to decline whereas offspring survival is predicted to remain constant. We suggest two potential explanations but presently lack the data to test these hypotheses: 1) mothers in the oldest age classes may experience declines in body mass but still remain above a threshold body mass to wean offspring with probability of survival equal to a prime aged mother, or 2) mothers in the oldest age classes may compensate for declines in body mass by investing proportionally more body mass into offspring (terminal investment hypothesis, Gadgil and Bossert 1970, Pianka and Parker 1975) and thus, wean proportionally larger offspring with survival rates equal to those of young produced by prime-aged mothers.

Female body mass declined amongst the oldest age classes, suggesting the existence of important changes in age-specific reproductive potential. Senescent related declines in reproductive performance have been documented in many long-lived animals

(Weimerskirch 1992, Packer *et al.* 1998, Mysterud *et al.* 2001, Bowen *et al.* 2006), and declines in body mass may precede declines in reproduction (Bérube *et al.* 1999). Maternal body condition and size can influence many aspects of female reproduction, including the ability to conceive (Samson and Huot 1995), offspring size (Arnbom *et al.* 1997, Wheatley *et al.* 2006), and offspring survival rate (Atkinson and Ramsay 1995). A reduction in body mass of senescent females could therefore affect either reproductive rate or offspring viability. Bighorn sheep (*Ovis canadensis*) ewes, which can live to be 19 years old, experienced declines in body mass at 11 years of age, and lamb production decreased following the age-related decrease in body mass (Bérube *et al.* 1999). Recent studies on grey seals (*Halichoerus grypus*), documented senescent declines in multiple measures of reproductive performance (apparent birth rate, offspring birth mass, lactation duration, offspring weaning mass) but no declines in maternal body mass, suggesting senescent declines in ovarian function and/or physiological function associated with milk production and transfer (Bowen at al. 2006). Evidence from the Weddell seal suggests that reduction of body mass of senescent females (this study) may affect offspring size at independence (Wheatley *et al.* 2006) and potentially offspring viability (Hadley *et al.* 2007, Proffitt *et al.* in review).

Further, we found that variations in large-scale atmospheric oceanographic variations produced variations in body mass that were of equal magnitude to age-related variations in body mass, suggesting that stochastic processes may also be an important component of Weddell seal reproductive performance. Environmental conditions during the summer of pregnancy affected maternal body mass at parturition, and body mass was higher following summers with low sea-ice extent and positive phases of the southern

oscillation. The consequences of environmentally induced variations in maternal body mass are manifested in post-partum energetic expenditure, and affect offspring size (Wheatley *et al.* 2006), condition at weaning (Wheatley *et al.* 2006), and survival probability (Proffitt *et al.* 2008). Both pup weaning mass and cohort survival show high annual variability (Cameron and Siniff 2004, Hadley *et al.* 2007, Proffitt *et al.* 2007), and environmental variations influencing maternal body mass at parturition may affect a mother's annual reproductive performance and offspring survival probability.

Environmental variations can have profound effects on the biotic components of marine ecosystems (Walther *et al.* 2002, Weimerskirch *et al.* 2003). We found evidence that variations in sea-ice extent and the state of the Southern Oscillation affected foraging success (as indexed by maternal body mass) of pregnant Weddell seals. Although the effects of the Southern Oscillation on Antarctic ecosystems are not well understood (Stenseth *et al.* 2002, Turner 2004), mounting evidence suggests that variations in the Southern Oscillation and sea-ice extent may have important affects on Antarctic top-trophic species (Testa *et al.* 1991, Ainley *et al.* 1998, Barbraud and Weimerskirch 2001a, Barbraud and Weimerskirch 2001b, Vergani *et al.* 2001, Proffitt *et al.* 2007).

Variations in sea-ice extent have been linked to the diet composition of Adelie penguins in a nearby by study area (20-50km away), and *Pleuragramma antarcticum,* the primary prey of Weddell seals, was more prevalent in Adélie diet during summers of reduced sea-ice extent (Ainley *et al.* 1998). Our finding that seal body mass was higher following summers with reduced sea-ice extent is consistent with the hypothesis that *Pleuragramma* abundance and availability to top predators is correlated with sea-ice extent. Interactions between trophic levels within the Ross Sea ecosystem are not well

understood, but in general, the food web is substantially different than most other areas of the Southern Ocean, with *P. antarcticum* playing a critical role in food web dynamics (La Mesa *et al.* 2004, Smith *et al.* 2007). We suggest that variations in summer sea-ice extent, which affect the timing and magnitude of the phytoplankton bloom (Arrigo and van Dijken 2004), may affect the availability of *Pleuragramma* to top predators in the Ross Sea and may be an important factor in the body mass dynamics and reproductive performance of upper-trophic-level species. The climate in the Ross Sea region of Antarctica is changing (Vaughn *et al.* 2001, Doran *et al.* 2002). Therefore, understanding relationships between physical and biological components of this ecosystem are increasingly valuable and will contribute to an overall understanding of the structure and function of the Ross Sea ecosystem.

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CHAPTER 3

EXPLORING LINKAGES BETWEEN ABIOTIC OCEANOGRAPHIC PROCESSES AND A TOP TROPHIC PREDATOR

Abstract

Climatic variation affects the physical and biological components of ecosystems, and global-climate models predict enhanced sensitivity in polar regions, raising concern for Antarctic animal populations that may show direct responses to changes in sea-ice distribution and extent, or indirect responses to changes in prey distribution and abundance. Here, we show that over a thirty-year period in the Ross Sea, average weaning masses of Weddell seals, *Leptonychotes weddellii*, varied strongly among years and were correlated to large-scale climatic and oceanographic variations. Annual weaning mass (a measure of the foraging success of pregnant seals) increased following summers characterized by reduced sea-ice cover and positive phases of the southern oscillation. These results demonstrate a correlation between environmental variation and an important life history characteristic (weaning mass) of an Antarctic marine mammal. Understanding the mechanisms that link climatic variation and animal life history characteristics will contribute to understanding both population dynamics and global climatic processes. For the world's most southerly distributed mammal species, the projected trend of increasing global climate change raises concern because increasing sea-ice trends in the Ross Sea sector of Antarctica will likely reduce populations due to reduced access to prey as expressed through declines in body condition and reproductive performance.

Introduction

Environmental variation can have profound effects on the biotic components of marine ecosystems (Walther *et al.* 2002, Weimerskirch *et al.* 2003). However, the uncertainty over the nature of linkages between physical and biological process prevents knowledgeable prediction of the potential effects of future environmental change (Croxall 1992). Warming of the earth's climate and oceans has been well documented over the last half century (Houghton *et al.* 2001, Gille 2002, Levitus *et al.* 2000), and global climate models predict enhanced sensitivity in polar regions due to albedo – polar ice cover – temperature feedback loops (Kellogg 1975, Parkinson 2004). Climatic changes in the south polar regions may have far reaching effects on biological processes, as recent evidence suggests that subantarctic mode water, which spreads throughout the entire southern hemisphere and north Atlantic oceans, is the main source of nutrient export from surface waters to the thermocline and deep waters (Sarmiento *et al.* 2004). Analysis of top-trophic species' population dynamics may be useful in understanding linkages between physical and biological components of ecosystems because changes in their population dynamics may amplify the effects of environmental variation on lower trophic levels, providing an integrative view of the ecological consequences of environmental variation (Croxall *et al.* 2002, Jenouvrier *et al.* 2005).

Extensive sea-ice cover in Antarctica and the surrounding Southern Ocean has numerous impacts on the biotic components of these marine ecosystems (Loeb *et al.* 1997, Barbraud and Weimerskirch 2001) and plays a critical role in global climate (Gille 2002). Spatially and temporally, regional sea-ice extent shows large intra- and inter-

annual variations, and is correlated with variations in the distribution and abundance of phytoplankton, Antarctic krill and top-trophic predators (Loeb *et al.* 1997, Nicol *et al.* 2000, Barbraud and Weimerskirch 2001). Furthermore, Antarctic sea-ice and Southern Ocean ecosystems are affected by large scale ocean-atmospheric variations associated with the ENSO signal that produces changes in sea surface temperatures and current patterns (Kwok and Comiso 2002). Although the relationships between ENSO and marine ecosystems in the tropics and high latitude areas in the Northern Hemisphere have received considerable attention, we are only in the early stages of understanding how ENSO affects Antarctic ecosystems (Testa *et al.* 1991, Turner 2004). Ocean-atmospheric variations in the southern ocean are further influenced by the Southern Annular Mode which is a pattern of non-seasonal circulation variability effecting the strength and location of the Antarctic circumpolar current, as well as sea-ice conditions (Lefebvre *et al.* 2004)

Regionally, Antarctic climate change is complex and trends are not uniform (Vaughan *et al.* 2001)**.** Rapid regional warming and retreat of ice shelves on the Antarctic Peninsula is well documented and has been linked to changes in seabird population dynamics, distribution, and abundance (Fraser *et al.* 1992, Vaughan and Doake 1996, Smith *et al.* 1999, Croxall *et al.* 2002, Vaughn *et al.* 2003, Domack *et al.* 2005). Long-term ecological studies along the Antarctic Peninsula have provided the rare opportunity to observe how changes in the physical environment are related to biological changes in the marine ecosystem (Fraser *et al.* 1992, Smith *et al.* 1999, Croxall *et al.* 2002). However, regional climate trends differ in the Ross Sea sector of Antarctica and ecological responses are unknown. In contrast to the warming temperatures and

declining sea-ice trends along the Antarctic Peninsula, the Ross Sea sector of Antarctica has experienced cooling temperatures, increasing sea-ice extent, and a lengthening sea-ice season (Vaughan and Doake 1996, Stammerjohn and Smith 1997, Vaughn *et al.* 2001, Doran *et al.* 2002, Zwally *et al.* 2002, Parkinson 2004). The Ross Sea is one of the most biologically productive regions of the southern ocean (Arrigo *et al.* 1998) and has largely escaped anthropogenic alteration (Ainley 2003), providing a rare opportunity to investigate the ecological responses of an unaltered system to environmental variations.

In this chapter, we investigate the influences of environmental variations in the Ross Sea sector of Antarctica on an important life history characteristic of a top-trophic level predator, the Weddell seal. The Erebus Bay Weddell seal population in the Ross Sea is one of the longest studied marine mammal populations in the world and pup weaning mass measurements have been collected periodically over three decades (Siniff *et al.* 1977, Testa and Siniff 1987, Cameron and Siniff 2004). Pup weaning masses reflect the foraging success of parturient females during the previous year and may vary with annual changes in environmental conditions and ocean processes that affect marine food webs and prey availability (Vergani *et al.* 2001, Le Boeuf and Crocker 2005, McMahon and Burton 2005). Understanding relationships between environmental variation and ecological responses will contribute to understanding linkages between global climatic and biological processes.

Methods

Study Population

The study population reported on here occupies Erebus Bay, located in the western Ross Sea, Antarctica, and is the most extreme southern location of any mammal population in the world. The Erebus Bay Weddell seal population size declined to low levels in 1976-78, and has remained relatively stable since 1979 (Testa and Siniff 1987). The population is likely open and part of a larger metapopulation, as fluctuations in population size are suspected to be influenced by annual variation in immigration and emigration (Cameron and Siniff 2003). However, the importance of exchange with other populations is unknown until work currently underway on the topic (Rotella and Garrott, unpublished data) is completed. Annually, from late October to November, approximately 400 Weddell seals produce pups in the study area. From 1969 to the present, Weddell seal pupping colonies have been monitored annually, and weaning masses of pups were frequently recorded. Pup weaning mass is closely linked to maternal condition because the energetic costs of lactation are supported solely by the females' stored energy reserves which are accrued during the pregnancy period and pups do not feed independently prior to weaning (Oftedal *et al.* 1987). Previous research at this study site has focused on many aspects of Weddell seal population ecology (Stirling 1969, Siniff *et al.* 1977, Testa and Siniff 1987, Castellini *et al.* 1992, Hastings *et al.* 1999, Cameron and Siniff 2004).

Response Variable

Weaning masses were collected periodically over a thirty-one year period from 1974 to 2004. Each year that data were available, mean annual weaning mass was estimated, and years with $n < 15$ were censored from analyses. The minimum sample size of 15 was selected because the standard error about the annual mean mass became quite stable for sample sizes this large and above. Lower sample sizes produced imprecise mean mass estimates, which would have reduced our ability to detect relationships. A random sample of pups was measured each year, and we assume the annual mean weaning mass that we estimated was representative of the population mean weaning mass. Although masses were measured at different colonies between and within years, our previous analyses do not indicate any inter-colony variation in average pup weaning mass (this study, unpublished data). Weaning mass was defined as either 1) the mass of an animal between day 35 and day 48 if the animal was weighed only one time in the later stages of the nursing period (85% of all measurements), or 2) the maximum mass that was recorded for an animal between day 35 and day 48 if the animal was weighed two times during the later stages of the nursing period (15% of all measurements). Further, in each of the four years (1975, 1980, 1984, and 1992) in which multiple mass measurements were collected, < 40% of the individual masses were from multiple measurements. Thus, variations in methodology would have little likelihood of producing a systematic bias that would influence the evaluation of environmental drivers of mean weaning mass. Mass was measured using one of two methods: by rolling the pup into a sling and weighing using a spring scale suspended from a pole resting on the shoulders of two researchers (1974-1983 and 1987-2004), or by coercing the animal onto

a digital weight platform (1984-1987 data, Steer Engineering, Ltd., Victoria, Australia). A total of 10 years were included in the analysis (2004 was censored because environmental covariates were not available).

Environmental Covariates

We considered three types of climate covariates: sea-ice extent in the Ross Sea sector of Antarctica (Comiso 1999, National Ice Center 2005), the Southern Oscillation Index (Bureau of Meteorology 2005), and the Southern Annular Mode (http://www.jisao.washington.edu/). Climate covariates were measured during the summer and winter of the pregnancy period (approximately Dec – Sept), and correlated to weaning masses the following pupping season. Summer sea-ice extent was measured in the first week in February (approximate timing of minimum sea-ice extent, MinExtent) and winter sea-ice extent was measured in the first week of September (approximate timing of maximum sea-ice extent, MaxExtent). Summer (Dec – Feb, SumSOI) and winter (Jul – Sept, WinSOI) SOI were calculated as three month running averages to avoid the noise due to small-scale and transient phenomena that are not associated with the large-scale coherent southern oscillation signal (Kwok and Comiso 2002). Southern Annular Mode was calculated as the three month summer mean (Dec – Feb, SumSAM) and three month winter mean (Jul-Sept, WinSAM). All variables were centered and scaled prior to analyses. We hypothesized that variations in weaning masses were primarily related to summer environmental conditions that may influence the amount of open water, primary production, and prey available to pregnant seals. We predicted increased summer sea-ice extent associated with positive summer SOI values (Kwok and

Comiso 2002) and positive summer SAM values (Lefebvre *et al.* 2004) may decrease forage fish availability, possibly through the reduction of primary productivity or changes in ocean circulation, reducing maternal foraging success and producing lower weaning masses among Weddell seals the following spring.

Model Development and Evaluation

Hypotheses about the potential effects of environmental variation on pup weaning mass were formulated and expressed as a set of candidate models, and a bias-corrected version of Akaike's Information Criterion, AIC_c, was used to rank hypothesized models (Burnham and Anderson 2002). Our candidate model list included every combination of one, two, three, four, five and six predictor models ($n = 62$), but given the limited weaning mass data available we did not include any interactions. Akaike model weights (w_k) were computed and used to address model-selection uncertainty (Burnham and Anderson 2002). We employed a linear modeling approach to evaluate all a priori models. Additionally, because there was some uncertainty in the response variable, average annual weaning mass, we compared the coefficient estimates from the top model with estimates computed using a weighted least squares modeling approach and weighting observations by the inverse of their variance.

Four functional forms of each covariate were considered when expressing hypotheses as statistical models: linear, pseudo-threshold, exponential, and moderated (Sydeman *et al.* 1991, Franklin *et al.* 2000). The linear form predicted a fixed value increase or decrease in the response per unit increase x_i, and was expressed $\beta_i x_i^*$, where $x_i^* = x_i$. The asymptotic form predicted the response approached but never reached an

asymptote as x_i increased, and was expressed as $\beta_i x_i^*$, where $x_i^* = \ln(x_i)$. The exponential form predicted an unlimited increase or decrease in the response variable as the x_i increased, and was expressed as $\beta_i x_i^*$, where $x_i^* = \exp(x_i)$ (Bruggeman *et al.* 2007). The moderated form predicted an increased or decreased response per unit increase in x_i, and was expressed as $\beta_i x_i^*$, where $x_i^* = (x_i)^{1/2}$. A sequential model-fitting technique was used to fit the data to candidate *a priori* model structures and the four functional forms. Variance inflation factors, which measure the degree of multi-colinearity, were calculated for all predictor variables, and any predictor that had a factor of 5 or greater was discarded from the analyses. To assess the relative importance of each predictor variable, we calculated a predictor weight for each of the R predictors, $w_{+(j)}$, by summing Akaike weights for all *a priori* models containing predictor x_j, for $j = 1, \ldots, R$ (Burnham and Anderson 2002).

Results

The weaning mass of 586 pups were collected from 1974 – 2004. Annual mean weaning mass ranged from 92.74 – 124.24 (range n = 18 - 107), and varied significantly among years (Figure 3.1, ANOVA, df = 9, $p < 0.001$). Summer minimum sea-ice extent (MinExtent) ranged from 3.2×10^5 to 11.3×10^5 km^2 (CV = 0.43) and winter maximum sea-ice extent (MaxExtent) ranged from 3.6×10^6 to 4.3×10^6 (CV = 0.06). Summer Southern Oscillation Index (SumSOI) ranged from -17.1 to 8.2 (CV = 0.42) and winter Southern Oscillation Index (WinSOI) ranged from -17.5 to 21.4 (CV = 0.74). Summer Southern

Annular Mode (SumSAM) ranged from -53.0 to 137.7 (CV = 0.37) and winter Southern Annular Mode (WinSAM) ranged from -58.3 to 182.7 (CV = 0.26).

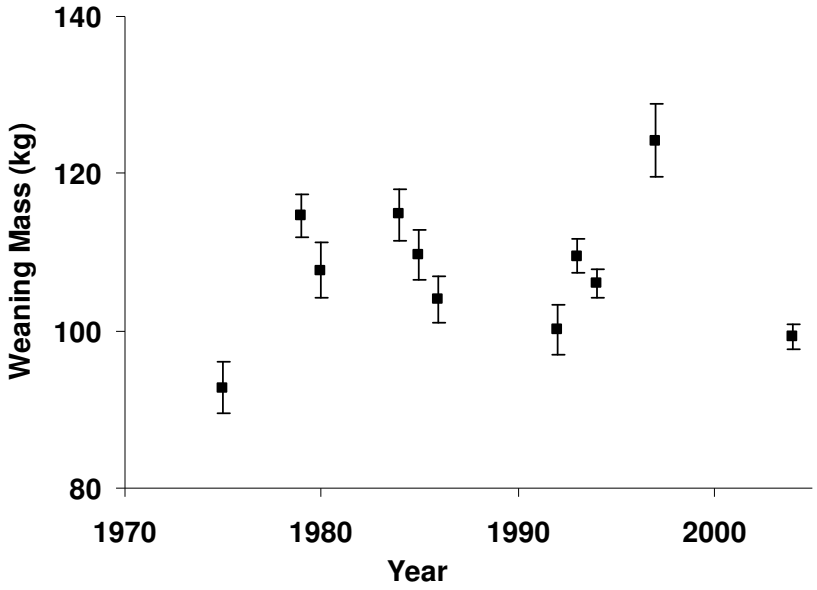


Figure 3.1. Annual variation in mean weaning mass (range n = 18–107) of Weddell seal pups in the western Ross Sea, Antarctica. Error bars denote ± 1 standard error.

Two models had $\Delta AIC_c < 2$ and received the greatest support in our modeling exercise. The best approximating model included the covariates MinExtent and SumSOI and received an Akaike weight of 0.64 (Table 3.1).

Table 3.1. Model selection results for *a priori* models examining the effects of environmental covariates on variation in Weddell seal pup weaning mass. Covariates evaluated include summer minimum sea-ice extent (MinExtent), winter maximum sea-ice extent (MaxExtent), summer Southern Oscillation Index (SumSOI), winter Southern Oscillation Index (WinSOI), summer Southern Annular Mode (SumSAM), and winter Southern Annular Mode (WinSAM). The top four *a priori* models are presented along with the number of parameters (K), the ΔAIC_c value, and the Akaike weight (w_k). The AIC_c value for top model was 63.0580.

Model	*Model Structure*	*K*	ΔAIC_c	w_k
1	β0 + β1(expMinExtent) + β2(expSumSOI)	3	0.00	0.65
2	β0 + β1(expMinExtent) + β2(expSumSOI) + β3(expWinSAM)	4	1.91	0.29
3	β0 + β1(expMinExtent) + β2(expMaxExtent) + β3(expSumSOI)	4	4.95	0.05
4	β0 + β1(MinExtent)+ β2(MaxExtent)+ β3(SumSOI)+ β4(WinSAM)	5	7.50	0.02

These covariates explained 86% of the annual variation in weaning mass. The second best model included covariates MinExtent, SumSOI, and WinSAM and received an Akaike weight of 0.25. Each of the top model structures AIC_c values were reduced by transforming the predictor variables to the exponential form. Exploratory plots of the non-transformed data showed non-linear trends validating the transformation. Relative to the other predictors that were considered, MinExtent and SumSOI, were the two best predictors of pup weaning masses (Table 3.2). MinExtent had a negative effect and SumSOI had a positive effect on weaning mass, but contrary to our predictions SumSAM had no significant effect on our best approximating models.

Table 3.2. Coefficient values and standard errors from the two top models selected using AIC_c model comparison techniques examining annual variation in Weddell seal pup weaning masses. Bold notation denotes coefficients significant at α = 0.05. Predictor weights ($w_{+(i)}$) are presented for the overall modeling exercise.

Covariate	$w_{+(i)}$	*Model*	
		1	2
MinExtent	0.98	**-0.14 (0.03)**	**-0.14 (0.03)**
SumSOI	0.98	**0.25 (0.06)**	**0.26 (0.05)**
WinSAM	0.27	-	0.07 (0.04)

In the top two models, coefficient estimates calculated using a weighted least squares modeling approach were similar to unweighted coefficient estimates (Table 3.3) and the coefficient of determination decreased only slightly using the weighted least squares approach (regular least squares R^2 = 0.86 and 0.85; weighted least squares R^2 = 0.89 and 0.88).

Table 3.3. Coefficient values and standard errors from the two top models estimated using a weighted least squares approach. Bold notation denotes coefficients significant at α = 0.05.

Covariate	*Model*	
	1	2
MinExtent	**-0.14 (0.03)**	**-0.13 (0.03)**
SumSOI	**0.24 (0.06)**	**0.26 (0.06)**
WinSAM	-	0.07 (0.04)

Discussion

Variation in a large scale oceanographic event (ENSO as measured by SOI) and summer sea-ice conditions were the primary drivers of annual variation in pup weaning mass. Weaning masses were highest following pregnancy periods characterized by low sea-ice extent and a strong positive summer southern oscillation. These results are consistent with results of Vergani *et al.* (2001) that showed southern elephant seal

weaning masses were higher during positive phases of the southern oscillation and with results of Testa *et al.* (1991) that showed Weddell seal reproductive rate was higher during positive phases of the southern oscillation. These studies suggest that ENSO events may influence prey availability and the foraging success of pregnant seals. We have found indirect evidence which suggests environmental variations influence the foraging success of pregnant Weddell seals which is reflected in subsequent weaning mass of their offspring. Testa *et al.* (1991) presented hypotheses more than a decade ago that large scale oceanographic variations related to ENSO may be related to Antarctic seal population dynamics, however the temporal scale over which these large scale environmental variations operate require long term datasets which are rare and, until recently, have been unavailable.

Summer sea-ice extent was a strong predictor of annual weaning mass, and masses were higher in pupping seasons following summers with low sea-ice extent (i.e. more extensive open water). In the Ross Sea, reduced summer sea-ice extent results in an earlier phytoplankton bloom and increased phytoplankton production (Arrigo and van Dijken 2004), which may influence the abundance and distribution of mid-level consumers and prey available to pregnant seals. The diet composition of Adélie penguins in a nearby study area (20-50 km away) was shown to change with variations in sea-ice extent (Ainley *et al.* 1998). In years with reduced sea-ice cover *Pleuragramma antarcticum* became more prevalent in the Adélie diet, suggesting that fish abundance and sea-ice extent may be negatively correlated. The abundance of *Pleuragramma* may be influenced by prey abundance (euphausiids and copepods, Hubold 1985), which is linked to the extent of sea-ice and the level of primary productivity. *Pleuragramma* is the

primary prey of Weddell seals (Burns *et al.* 1998), and if *Pleuragramma* abundance is tied to the extent of open water, than it is likely that pregnant seals experience improved foraging conditions (higher prey abundance) in years of more extensive open water. Direct assessments of annual variation in the abundance of mid-trophic level species such as krill and *Pleuragramma*, and their population dynamics are necessary to enhance our understanding of ecosystem processes in the Ross Sea.

The heterogeneity in environmental conditions in early life has the potential to induce fitness differences between cohorts (Lindstrom 1999), and may have an impact on later survival and reproductive performance. It has been well documented that larger offspring have increased survival in diverse species of marine and terrestrial mammals (Baker and Fowler 1992, Clutton-Brock *et al.* 1992, Craig and Ragen 1999, McMahon and Burton 2000, McMahon and Burton 2005). Thus, climatic variation that influences maternal foraging success and subsequent pup weaning mass likely has important effects on early survival and population dynamics. Our results show a clear and significant correlation between environmental variation and mean cohort weaning mass, but we have yet to relate individual and/or cohort weaning mass to juvenile survival. Developing linkages between environmental variation, weaning mass, and demographics is difficult because weaned pups do not return to the study area until they are recruited into the population between age five and ten, and long-term studies such as this are required to collect the necessary data. We hypothesize Weddell seal weaning mass may not only correlate to environmental variations, but may also influence juvenile survival. If these hypotheses prove correct, then body mass may be a mechanism that links environmental

variation and population dynamics and may be a useful index of the state of the marine ecosystem.

Much attention in global climate change literature has focused on the detrimental effects of warming and declining sea-ice extent. However, the Ross Sea sector of Antarctica is experiencing cooling trends with increasing sea-ice extent (Vaughan and Doake 1996, Stammerjohn and Smith 1997, Vaughn *et al.* 2001, Doran *et al.* 2002, Zwally *et al.* 2002), conditions that may decrease foraging success and haul-out opportunities for seals. In addition, a cooling trend may result in a reduction in the frequency and extent of annual fast ice breakout in the southern sectors of the Ross Sea, resulting in the accumulation of thick multiyear ice that may limit Weddell seals' access to the sea-ice surface for pupping. Recently, due to the presence of the large iceberg, B-15A (~6,4000 km^2), ice advection has been restricted and multi-year ice is more extensive in this study area. In 2004, we recorded approximately half the number of adult female seals present at pupping colonies, and pup numbers were only 40% of the long-term mean. This low level of reproduction was well below the range of annual variation for the past 34 years, and may indicate another mechanism that will likely reduce the demographic vigor of Weddell seals if cooling trends continue (Garrott *et al.* 2005). These results are amongst the first to report on the ecological consequences of localized climate cooling, and broaden understanding of the full consequences of global climate change.

Future investigations should evaluate the effects of both environmental variations and maternal characteristics on pup weaning mass. Factors such as maternal age, maternal parturition mass, parity or pup sex may effect individual weaning masses (Hill

1987, Arnbom *et al.* 1997, Bowen *et al.* 2001, Crocker *et al.* 2001), and accounting for these effects may eliminate noise in the data and further clarify the relationships between mass and environmental variations. Long-term investigations such as this will be necessary to evaluate maternal characteristics and account for these relationships.

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CHAPTER 4

LONG-TERM EVALUATION OF BODY MASS AT WEANING AND POST-WEANING SURVIVAL RATES OF WEDDELL SEALS IN EREBUS BAY, ANTARCTICA

Abstract

Variability in juvenile survival rate is expected to be an important component of the dynamics of long-lived animal populations. Across a range of species, individual variation in juvenile body mass has been shown to be an important cause of variation in fates of juveniles. Our goal in this paper was to estimate age-specific apparent survival rates for Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica, and to investigate hypotheses about relationships between body mass at weaning and apparent survival rate for juveniles. Mark-resighting models revealed positive relationships between body mass at weaning and apparent juvenile survival rate (survival from weaning to age 3). Average apparent juvenile survival rate was similar between males and females, but the effects of body mass on juvenile survival rate differed between the sexes, and the relationship between body mass and survival rate was stronger in males. These results indicate that energy transferred from mother to pup during lactation, which determines body mass at weaning, is important in determining offspring survival rate, and suggest that maternal traits and environmental variations that affect the magnitude of energy delivered to offspring during lactation likely have important consequences on offspring survival rate, individual fitness, and population dynamics.

Introduction

Understanding variation in basic demographic parameters, such as survival rate, is fundamental to understanding population dynamics of long-lived animals. In long-lived vertebrates with delayed maturity, population annual growth rate (λ) shows high elasticity to adult survival rate and low elasticity to juvenile survival rate (Gaillard *et al.* 2000, Saether and Bakke 2000, Gaillard and Yoccoz 2003). In accordance, the demographic buffering hypothesis predicts that fitness components having the greatest potential impact on λ should be the least variable through time, while those with less potential impact on λ are predicted to show higher temporal variability (Pfister 1998, Gaillard *et al.* 2000). Adult survival rate is therefore expected to be relatively constant, whereas juvenile survival rate is expected to show higher annual variability, reflecting the population's response to density dependent factors and environmental variability (Gaillard *et al.* 1998, Eberhardt 2002, Gaillard and Yoccoz 2003). If this predicted pattern occurs, then temporal variation in juvenile survival rate due to annual variation in environmental conditions will be an important component of annual variation in population dynamics (Coughenour and Singer 1996, Gaillard et al 1998, Gaillard *et al.* 2000).

Juvenile survival rate may be influenced by predation, parasites, or environmental variation which lead to changes in food supply and body condition (Wickens and York 1997), and juveniles may be more sensitive to environmental variability because of immature immune systems or lack of experience (Gaillard *et al.* 1998, Gaillard and Yoccoz 2003). Possible mechanisms by which environmental variation may influence juvenile survival rate include direct influences such as food availability and foraging

success and indirect influences such as stored maternal reserves and energy transfer during lactation (McMahon and Burton 2005). Among capital breeding species, maternal body mass at parturition is influenced by environmental variation affecting maternal foraging success. Consequently, offspring body mass at weaning shows inter-annual variation that correlate with environmental conditions (Vergani *et al.* 2001, LeBoeuf and Crocker 2005, McMahon and Burton 2005, Proffitt *et al.* 2007a, Proffitt *et al.* 2007b). In addition, recent studies have shown that first-year survival rate is correlated with annual variation in environmental conditions (Beauplet *et al.* 2005, McMahon and Burton 2005) which suggests that body mass may, through its affects on juvenile survival rate, link environmental conditions and population dynamics.

Across a range of species, pre-weaning growth rate, body size, or body mass are positively correlated with juvenile survival rate (Guinness *et al.* 1978, Murie and Boag 1984, Baker and Fowler 1992, Sedinger *et al.* 1995, Festa-Bianchet *et al.* 1997, Beauplet *et al.* 2005). Amongst phocid seals, pre-weaning body condition or body mass and post-weaning survival rate may be correlated, with animals in higher body condition or of higher body mass having higher post-weaning survival (southern elephant seal (Mirounga leonina), McMahon *et al.* 2000, McMahon and Burton 2005, grey seal (Halichoerus grypus), Hall *et al.* 2001). For species such as these that are abruptly weaned, the amount of resources accrued prior to weaning may be important in sustaining pups through the transitional period from maternal dependence to nutritional independence and may be important in determining subsequent survival (Hall *et al.* 2001). Additionally, larger pups may have greater diving capabilities (Burns 1999, Hindell *et al.* 1999) and lose less heat due to their higher blubber content (Bryden 1964). Thus, larger pups are expected to

have an advantage over their smaller counterparts by being able to spend more time searching for food during their first months of nutritional independence (McMahon *et al.* 2000, Beauplet *et al.* 2005).

Here, we evaluate age-specific apparent survival rate of Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica, and investigate potential relationships between body mass at weaning and apparent juvenile survival rate. Long-term demographic studies on this population have been underway since 1968 (Siniff *et al.* 1977, Testa and Siniff 1987, Cameron and Siniff 2004), and we used data collected over the past three decades to estimate age-specific apparent survival rate and to evaluate relationships between body mass at weaning and apparent juvenile survival rate (survival from weaning to age 3). We evaluated weaning mass and sex as covariates potentially affecting apparent survival rate in juvenile Weddell seals. Weaning masses are highly variable, showing up to two-fold variations among individuals, and a pup's weaning mass is related to its mother's parturition mass (Wheatley *et al.* 2006) and annual environmental conditions (Proffitt *et al.* 2007a). Differences in male and female juvenile survival rate are reported in many mammalian species (Garrott 1991, Hall *et al.* 2001, Mathisen *et al.* 2003, Beauplet *et al.* 2005), including the Weddell seal (Hastings *et al.* 1999), with juvenile males showing lower survival than females.

We predicted that apparent juvenile survival rate would be positively related to body mass at weaning but that this relationship might be non-linear. Accordingly, we considered two functional forms of the relationship: linear (directional selection hypothesis) and quadratic (stabilizing selection hypothesis). Positive linear relationships between survival rate and body mass reported in previous studies, predict selection would

favor evolution of larger body sizes (directional selection hypothesis). Larger females often produce greater numbers of offspring or offspring of better condition than smaller females, and larger males often have greater mating and reproductive success than smaller males (Honek 1993, Clutton-Brock *et al.* 1982, Clutton-Brock 1988, Shine 1989). Thus, it is widely agreed that fecundity selection and sexual selection are the major evolutionary forces that select for larger body sizes (Blanckenhorn 2000). The equilibrium view proposes that selection for larger body size is counterbalanced by opposing selective forces (see Blanckenhorn 2000 for review). Costs of being large may include increased predation or parasitism due to reduced agility or increased detectability, decreased mating success of males due to reduced agility or higher energy requirements, or decreased reproductive success of females due to later reproduction. Under the stabilizing-selection hypothesis, pups of average weaning mass are predicted to have higher survival rates than are pups of lower or higher mass. Finally, based on previous studies, we predicted that apparent survival rate would differ by sex, with survival rate being lower in males than in females.

Methods

Study Population

We studied individually marked Weddell seals at breeding colonies in Erebus Bay (western Ross Sea), Antarctica. Weddell seals are intermittent breeders and annually 300-600 females produce a single pup at breeding colonies in Erebus Bay. Pupping occurs on the fast ice surface from late October to November, and mother's remain in close association with pups throughout a 30-50 day lactation period. Females support the

energetic costs of lactation through mobilization of stored energy reserves (Boness and Bowen 1996), and neither mothers nor pups regularly feed during the lactation period. Lactation is followed by an abrupt weaning, after which pups receive no parental care. Maternal energetic investment during lactation and pup weaning masses closely correlate with maternal body mass at parturition (Hill 1987, Wheatley *et al.* 2006), and both parturition and weaning masses vary annually with variations in environmental conditions that may affect marine food resources (Proffitt *et al.* 2007a, Proffitt *et al.* 2007b).

From 1969 to the present, pups born within the Erebus Bay study area have been marked with individually numbered tags in the interdigital webbing of the rear flippers (Siniff *et al.* 1977) and since 1973, multiple annual systematic surveys of marked and unmarked Weddell seals have been conducted (approximately 5 surveys per season). At the time of tagging and during each resighting event, the date, location, tag number, and relative's tag number (if any) were recorded and added to the mark-resighting database. The majority of adults (both pupping and non pupping females, as well as males) return to traditional breeding colonies within the study area each year, and resighting rates are high (0.92 for females and 0.72 for males in a single survey, Cameron and Siniff 2004, 0.99 for nursing females estimated over multiple surveys, J.R. in prep). High fidelity to breeding colonies (Cameron *et al.* 2007) and high resighting rate allowed comprehensive resighting histories to be recorded for each marked animal.

Pup Weaning Mass Measurements

Weaning masses were collected periodically over a 33-year period from 1974 to 2006. Weaning masses were measured approximately 40 days post-parturition (range 35-45). Mass was measured using one of two methods: by rolling the pup into a sling and weighing using a spring scale or by coercing the animal onto a digital weight platform.

Mark-Resighting Models

We estimated apparent survival and sighting probabilities and evaluated relationships between covariates and these parameters using extensions of the Cormack-Jolly-Seber (CJS) models (Pollock *et al.* 1990, Lebreton *et al.* 1992) in Program MARK (White and Burnham 1999). All animals included in the analysis were initially marked as pups and their body masses were measured at weaning. We used resighting data collected during the 1974-2006 breeding seasons (Oct 1 – Dec 15) for pups marked from 1974 through 2004.

To evaluate our predictions, we developed a set of a priori models that included two types of parameters: apparent survival rate (ϕ) and resighting rate (p), where ϕ_i was defined as the probability that a seal alive in year i remains available for resighting until year i+1 (i.e., survives and does not permanently emigrate from the study area), and p_i was defined as the probability that a seal alive in year i that has not permanently emigrated is observed in year i. Our primary interest was in the effects of body mass at weaning on ϕ, however, it was important to also adequately model variation in ϕ and p.

Before evaluating models that considered individual covariates (sex and body mass at weaning), we first determined which of two age structures was most appropriate to use for modeling possible age-related variation in ϕ_i. Based on results of previous studies (Hastings *et al.* 1999, Cameron and Siniff 2004, Hadley *et al.* 2006), we compared models in which age structures for ϕ contained either 3 age classes (a3: 1-, 2-, and ≥3 year olds), or 6 age classes (a6: 1, 2, 3-6, 7-10, 11-14, and ≥15 year olds). However, because few yearlings were resighted during the study (n = 6), we constrained ϕ_i to be equal for 1- and 2-year olds in all models. This resulted in age structure for ϕ containing two and five age classes (a2: 1-2, and ≥3 year olds, a5: 1-2, 3-6, 7-10, 11-14, and ≥15 year olds). In all models, estimates of p_i were allowed to vary among four age-classes (a4: 1-, 2-, 3-6, and >7-year olds) (Hastings *et al.* 1999, Cameron and Siniff 2004, Hadley *et al.* 2007). We evaluated competing models to determine whether it was most appropriate to constrain age-specific estimates of p_i to follow linear or quadratic trends across age classes or to allow them to vary independently across age classes.

After determining the most appropriate age structure to use, we then evaluated the amount of support in the data for models that included effects of body mass at weaning (Mass) and sex of the animal (Sex). In our a priori models, Mass, in both linear and quadratic forms, was related to ϕ for 1- and 2-year old animals only, which expressed the prediction that high weaning mass would have the greatest benefits in the years immediately following weaning. We hypothesized that both ϕ and p might vary by animal sex because of strong sex-specific differences in behavior. Further, we predicted that p for males would be lower than that for females and that the difference would

increase with age because males guard underwater territories and are more likely to do so as they mature (Siniff *et al.* 1977, Hill 1987). Therefore, we evaluated models that allowed p to vary as a function of either additive or interactive affects of Sex and age (Age-Sex_{Add} and Age-Sex_{Int}, respectively). Although ϕ and p likely vary to some degree among cohorts and years (Cameron and Siniff 2004, Hadley *et al.* 2006), the annual sample sizes available for the analyses presented here prevented us from estimating cohort- or year-specific estimates.

We evaluated goodness of fit for the most general model that did not include individual covariates (included only age-structure) using a parametric bootstrap procedure in Program MARK (White *et al.* 2001), and estimated a variance inflation factor, $\hat{c}$, from 100 simulations. We adjusted AIC_c scores for overdispersion, and used $QAIC_c$ scores to compare models. Akaike model weights (w_k) were computed and used to address model-selection uncertainty (Burnham and Anderson 2002).

Results

Data were available for 486 animals marked as pups (238 males and 248 females), of which 109 (56 males and 53 females) were resighted in subsequent years. At least 1 pup was weighed at weaning in each of 17 years (average *n*/year = 28.6 pups, SD = 5.6). Annually, weaning mass averaged 105.8 kg (SE = 2.0). For those years in which at least 10 pups were weighed, average annual weaning mass ranged from a low of 81.9 kg (SE = 4.0) to a high of 119.6 kg (SE = 4.1). Weaning mass was similar for males (average = 106.2 kg, SD = 21.4) and females (average = 105.5 kg, SD = 19.6 kg).

A total of 24 a priori CJS models were evaluated, and $\hat{c}$ was 1.092 for the most general model that did not include either Mass or Sex, which indicated that for the most general model there was little overdispersion present and that reasonable goodness of fit was achieved. The data provided more support for models that estimated ϕ for five age classes and p as a quadratic function of four age classes (Table 4.1), Therefore, that age structuring of ϕ and p was included in all models used to evaluate effects of individual covariates on ϕ and p. For the top model that only considered age class, estimates of ϕ were 0.52 (SE = 0.03) for 1- to 2-year olds, 0.91 (SE = 0.02) for 3- to 6-year olds, 0.92 (SE = 0.02) for 7- to 10-year olds, 0.94 (SE = 0.03) for 11- to 14-year olds, and 0.73 (SE = 0.07) for animals >15 years old; and estimates of p were 0.03 (SE = 0.01) for 1-year olds, 0.15 (SE = 0.02) for 2-year olds, 0.43 (SE = 0.03) for 3- to 6-year olds, and 0.69 (SE = 0.03) for animals >7 years old.

Table 4.1. Model selection results for a priori models of variation in Weddell seal apparent survival rate (ϕ) and resighting rate (p). Age effects differed by parameter type: a2 indicated a 2-class age effect (ages 1-2, ≥3), a4 indicates a 4-class age effect (ages 1, 2, 3-6, ≥7), and a5 indicated a 5-class age effect (ages 1-2, 3-6, 7-10, 11-14, ≥15). Linear and quadratic trends in resighting rate are represented by LIN and QUAD. All models in the individual covariates suite were evaluated using the top ranked structure of ϕ and p from the model suite evaluating potential age-structure. Model structures, $\Delta QAIC_c$ value, Akaike model weight (w_k), and number of estimated parameters (K) are shown. $QAIC_c$ value for the top model was 1937.1 in the age-structure suite and 1887.7 in the effects of weaning mass and sex suite. Estimate of $\bar{\hat{c}}$ calculated from model ϕ_{a5}, p_{a4} was 1.092.

Model	$\Delta QAICc$	w_k	*K*
Suite Evaluating Potential Age-Structure			
$\phi_{a5}, p_{a4.QUAD}$	0.00	0.41	8
ϕ_{a5}, p_{a4}	0.49	0.32	9
$\phi_{a5}, p_{a4.LIN}$	1.60	0.18	7
$\phi_{a2}, p_{a4.QUAD}$	4.80	0.04	5
ϕ_{a2}, p_{a4}	5.35	0.03	6
$\phi_{a2}, p_{a4.LIN}$	6.08	0.02	4
Suite Evaluating Potential Effects of Weaning Mass and Sex			
$\phi_{\beta_0+\beta_1 Sex_A+\beta_2 Mass_M}, p_{\beta_0+\beta_1 Sex_I}$	0.00	0.21	14
$\phi_{\beta_0+\beta_1 Mass}, p_{\beta_0+\beta_1 Sex_I}$	1.01	0.13	13
$\phi_{\beta_0}, p_{\beta_0+\beta_1 Sex_I}$	1.24	0.12	12
$\phi_{\beta_0+\beta_1 Sex_A+\beta_2 Mass_M+\beta_3 Mass_M^2}, p_{\beta_0+\beta_1 Sex_I}$	2.05	0.08	15
$\phi_{\beta_0+\beta_1 Mass_F}, p_{\beta_0+\beta_1 Sex_I}$	2.14	0.07	13
$\phi_{\beta_0+\beta_1 Mass_M}, p_{\beta_0+\beta_1 Sex_I}$	2.16	0.07	13
$\phi_{\beta_0+\beta_1 Mass+\beta_2 Mass^2}, p_{\beta_0+\beta_1 Sex_I}$	2.45	0.06	14
$\phi_{\beta_0+\beta_1 Mass_M+\beta_2 Mass_M^2}, p_{\beta_0+\beta_1 Sex_I}$	2.89	0.05	14
$\phi_{\beta_0+\beta_1 Sex_A+\beta_2 Mass}, p_{\beta_0+\beta_1 Sex_I}$	3.05	0.05	14
$\phi_{\beta_0+\beta_1 Sex_A}, p_{\beta_0+\beta_1 Sex_I}$	3.28	0.04	13
$\phi_{\beta_0+\beta_1 Sex_A+\beta_2 MassF}, p_{\beta_0+\beta_1 Sex_I}$	3.63	0.03	14
$\phi_{\beta_0+\beta_1 Sex_A+\beta_2 Mass_F+\beta_3 Mass_F^2}, p_{\beta_0+\beta_1 Sex_I}$	4.23	0.03	15
$\phi_{\beta_0+\beta_1 Mass_F+\beta_2 Mass_F^2}, p_{\beta_0+\beta_1 Sex_I}$	4.27	0.03	14
$\phi_{\beta_0+\beta_1 Sex_A+\beta_2 Mass+\beta_3 Mass^2}, p_{\beta_0+\beta_1 Sex_I}$	4.49	0.02	15
$\phi_{\beta_0+\beta_1 Mass}, p_{\beta_0}$	49.24	0.00	10

Table 4.1 Contunued

Model	$\Delta QAICc$	w_k	*K*
$\phi_{\beta_0}, p_{\beta_0}$	49.37	0.00	9
$\phi_{\beta_0+\beta_1 Sex_A+\beta_2 Mass}, p_{\beta_0}$	50.76	0.00	11
$\phi_{\beta_0+\beta_1 Sex_A}, p_{\beta_0}$	50.91	0.00	10

The data provided support for our prediction that body mass at weaning is positively related to apparent survival rate for the first two years of life (ϕ_{juv}), particularly for male animals. The two top-ranked models both included weaning mass as a covariate related to ϕ_{juv} and together received 34% of the Akaike model weight (Table 4.1). In the top model, weaning mass was positively and linearly related to ϕ_{juv} (directional selection) for males ($\hat{\beta}_{Mass}$ = 0.007, SE = 0.003, 95% CI = 0.001 to 0.014) but not to ϕ_{juv} for females (Figure 4.1). For males, $\hat{\phi}_{juv}$ ranged from 0.44 (95% CI = 0.35 to 0.53) for a male that was 40 kg (minimum weaning mass in dataset) at weaning to 0.68 (95% CI = 0.53 to 0.81) for one that was 177 kg (maximum weaning mass in dataset). Based on parameter estimates from the top model, the estimated odds of a male pup surviving from weaning to age 3 increased 16.2% (CI = 2.0% to 34.9%) for every 21.4 kg increase in body mass accrued by weaning, where 21.4 kg was one standard deviation in the sample used in analysis. In the second-best model, weaning mass was positively and linearly related to ϕ_{juv} for both males and females ($\hat{\beta}_{Mass}$ = 0.007, SE = 0.005, 95% CI = -0.002 to 0.016). Thus, the point estimate for the mass coefficient remained the same, but the precision of the estimate decreased, and the confidence interval slightly overlapped zero. The third-ranked model, which was structured the same as the top model but with the Mass covariate removed, also received some support from the data ($\Delta QAIC_c$ = 1.24).

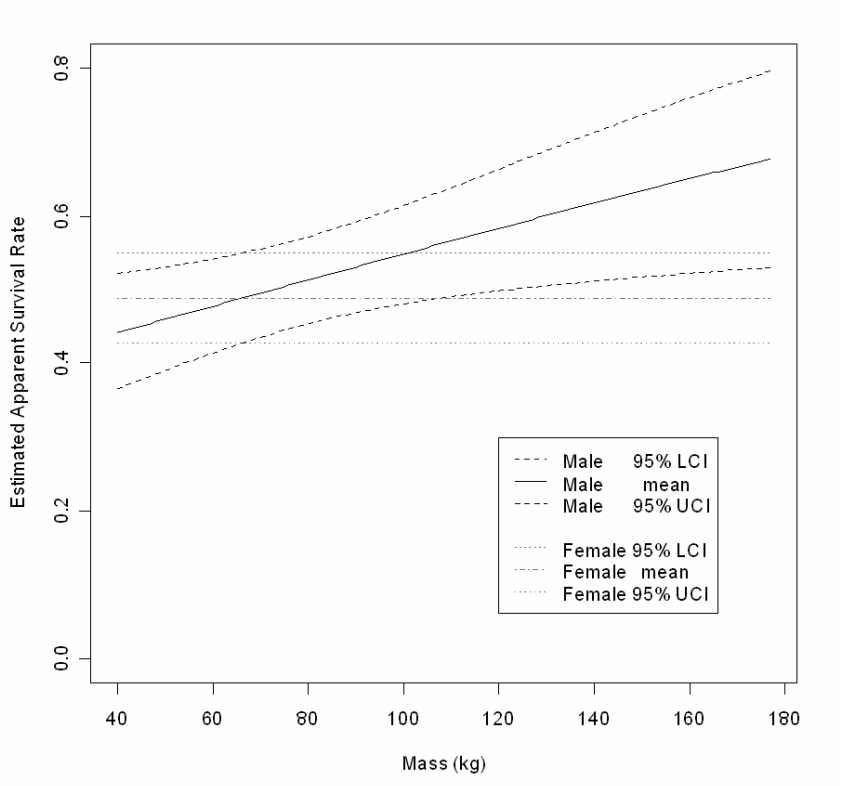


Figure 4.1. The estimated ϕ_{juv} for male and female Weddell seals in Erebus Bay, Antarctica as a function of their body mass at weaning. Estimates and 95% confidence intervals are generated from the top ranking model in the suite evaluating potential effects of weaning mass and sex ($\phi_{\beta_0+\beta_1 Sex_A+\beta_2 Mass_M}, p_{\beta_0+\beta_1 Sex_I}$, Table 1).

We found little support for our prediction that the relationship between body mass and survival rate was nonlinear. When the top model was modified such that Mass^2, as well as Mass, was related to ϕ_{juv} for males, the 95% confidence interval for $\hat{\beta}_{Mass^2}$ was almost perfectly centered about zero ($\hat{\beta}_{Mass^2}$ = 0.00001, 95% CI = -0.0001 to 0.0001) and the QAIC$_c$ score for the resulting model was 2.05 units worse than the value for the top model.

We did not find support for our prediction that ϕ_{juv} would be lower in males than in females. In fact, the top model provided evidence that all but the lightest males survive at a higher rate than do females (Figure 4.1). Based on estimates from our top model, $\hat{\phi}_{juv}$ was 0.56 (SE = 0.04, 95% CI = 0.48 – 0.63) for males of average mass (106.2 kg) and 0.49 (SE = 0.03, 95% CI = 0.43 to 0.55) for females regardless of their mass. Point estimates of ϕ_{juv} were >0.49 for males >69 kg, but when uncertainty of estimates was incorporated, confidence intervals of ϕ_{juv} were broad enough to preclude strong inferences regarding sex-specific differences in juvenile survival rate (Figure 4.1).

Exploratory analyses did not provide support for a relationship between body mass at weaning and survival rates in animals >3-years old. Finally, no exploratory models were found to fit the data better than a priori models ($\Delta QAIC_c > 8.5$).

Discussion

Body mass at weaning was found to be an important determinant of post-weaning survival rate, suggesting that maternal traits and environmental variation that affect the magnitude of energy delivered to offspring during lactation likely have important consequences on offspring survival rate and individual fitness. Mark-resight models revealed positive relationships between body mass at weaning and apparent survival rate of 1- and 2-year old Weddell seals, and the effects of body mass on apparent survival rate were more precisely estimated for male pups. These results indicate that energy transferred from mother to pup during lactation is important in determining offspring survival rate, and links energetic investment during lactation with a female's fitness.

Several studies, including an earlier study on Weddell seals, found sexual differences in juvenile survival rate, with males having a lower rate of survival than do females (Garrott 1991, Hastings *et al.* 1999, Hall *et al.* 2001, Beauplet *et al.* 2005). Although we found little evidence of differences in juvenile survival rate for males and females, we did find that male juvenile survival rate was more strongly influenced by body mass at weaning than female juvenile survival rate, which is consistent with findings from two previous seals studies. Hastings *et al.* (1999) found a positive relationship between reproductive rate (representing annual body condition of reproductive females) and male (but not female) first-year survival rate, suggesting that survival of male pups is more dependent upon maternal or environmental conditions than survival of females. A grey seal (*Halichoerus grypus*) study also found that the effects of body condition at weaning on survival rate was stronger in males than females (Hall *et al.* 2001). The effects of body condition at weaning may be more pronounced in male pups due to differences in metabolic activities, with males relying more heavily on lipid metabolism than females (Biuw 2003, Wheately *et al.* 2006) or to behavioral differences. The result that male juvenile survival rate is more sensitive to body condition at weaning predicts that high-quality females should invest more heavily in their male pups because the return, in terms of maternal fitness, from additional expenditure on male pups is greater than that for an investment in female pups (Hall *et al.* 2001).

Our finding that higher body mass at weaning resulted in higher post-weaning survival rate is consistent with findings from a variety of taxa (Guinness *et al.* 1978, Baker and Fowler 1992, Sedinger *et al.* 1995, Festa-Bianchet *et al.* 1997, McMahon 2000). We found a positive linear relationship between body size at weaning and

juvenile survival rate, and this relationship was stronger in males than females. These results support the directional selection hypothesis, however, in order for selection for larger body sizes to occur, traits coding for either larger body size or increased capacity for maternal energetic expenditure during lactation must be heritable and there must be no countervailing selection at another life stage. Although several marine mammal studies have found positive relationships between body mass or condition at weaning and post-weaning survival (Baker and Fowler 1992, McMahon 2000, Hall *et al.* 2001), the effects of body mass or condition at weaning and long-term survival and reproductive success are unknown. For Weddell seals, body mass at weaning was an important factor in juvenile survival (survival from weaning to age 3) but appeared to have little affect on survival rate later in life.

These findings also support the hypothesis that body mass may be a mechanism linking maternal traits such as age with patterns of reproductive performance (Hadley *et al.* 2007). Recent studies on this population have found that middle-aged and older mothers produce offspring with higher survival rates than those of their younger counterparts (Hadley *et al.* 2007). Maternal body mass at parturition, the primary determinant of offspring body mass at weaning (Hill 1987, Arnbom *et al.* 1997, Mellish *et al.* 1999, Crocker *et al.* 2001, Wheatley *et al.* 2006), is positively correlated with maternal age (Proffitt *et al.* 2007b), which yields the prediction that older, larger females produce larger offspring. Our findings that offspring with higher body mass at weaning (predicted to have older, larger mothers) had higher rate of survival than their smaller counterparts (predicted to have younger, smaller mothers) are consistent with predictions from previous studies that older, larger mothers produce offspring with higher survival

rate, and suggest that body mass may be an important mechanism linking maternal age and reproductive performance. These results have implications for understanding the reproductive strategy of female Weddell seals, and suggest that the costs of weaning larger, successful offspring may be higher for younger, smaller mothers.

Environmental variations influencing prey distribution and abundance may affect animals' body condition and be important factors to consider in the analysis of population dynamics. The diet composition, reproductive performance, and population dynamics of Antarctic top-trophic species may be affected by variations in sea-ice extent and the Southern Oscillation (Testa *et al.* 1991, Ainley *et al.* 1998, Barbraud and Weimerskirch 2001a, Barbraud and Weimerskirch 2001b, Vergani *et al.* 2001, Proffitt *et al.* 2007a). Based on our findings regarding the effects of body mass on survival rate, environmental variations that produce inter-annual variations in maternal parturition mass and offspring weaning mass will potentially affect offspring survival rate. Previous studies on this population have found annual variations in maternal body mass and offspring weaning mass correlate with variations in sea-ice extent and the Southern Oscillation (Proffitt *et al.* 2007a, Proffitt *et al.* 2007b). The findings of this study predict that environmental conditions resulting in reduced Weddell seal body mass (high sea-ice extent and a negative southern oscillation state) will reduce juvenile survival rate and negatively impact population growth. Understanding these linkages between large scale oceanographic-environmental variations and biological responses is increasingly important because the environment of the Ross Sea region of Antarctica is changing (Vaughn *et al.* 2001, Doran *et al.* 2002), and significantly altered biological dynamics, are expected should such changes continue (Smith *et al.* 2007).

We were unable to directly estimate the effects of environmental variations or cohort effects on apparent survival rate because of modest annual sample sizes. However, annual effects are likely important in explaining additional variation in survival rate (Hastings *et al.* 1999, Cameron and Siniff 2004, Beauplet *et al.* 2005). Future studies exploring linkages between annual variations in vital rates and environmental conditions are needed to clarify relationships between environmental variability and Weddell seal population dynamics. Additionally, future studies investigating the dispersion patterns of weaned seals may clarify the observed inter-sexual variations in relationships between body mass at weaning and juvenile survival rate.

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CHAPTER 5

THE IMPORTANCE OF CONSIDERING PREDICTION VARIANCE IN ANALYSES EMPLOYING PHOTOGRAMMETRIC MASS ESTIMATES

Abstract

Development and application of photogrammetric mass-estimation techniques in marine mammal studies is becoming increasingly common. When a photogrammetrically estimated mass is used as a covariate in regression modeling, the error associated with estimating mass induces bias in regression statistics and decreases model explanatory power. Thus, it is important to understand and account for prediction variance when addressing ecological questions that require use of estimated mass values. In a simulation study based on data collected from Weddell seals, we developed regression models of pup weaning mass as a function of maternal post-parturition mass where maternal mass was directly measured and second where maternal mass was photogrammetrically estimated. We demonstrate that when estimated mass was used the regression coefficient was biased towards zero and the coefficient of determination was 30% less than the value obtained when using maternal post-parturition mass obtained from direct measurement. After applying bias-correction procedures, however, the regression coefficient and coefficient of determination were within 2% their true values. To effectively use photogrammetrically estimated masses, prediction variance should be understood and accounted for in all analyses. The methods presented in this paper are effective and simple techniques to explore and account for prediction variance.

Introduction

There is increasing interest in body mass dynamics of marine mammals (Arnbom *et al.* 1997, Mellish *et al.* 1999, Bowen *et al.* 2001, Crocker *et al.* 2001, Beck *et al.* 2003, Schultz and Bowen 2004) as body mass may be correlated with life history traits (Peters 1983, Partridge and Harvey 1988, Roff 1992) and may be a sensitive indicator of resource availability (Croxall *et al.* 1988, LeBouef and Crocker 2005). Although the body mass of large mammals can be a difficult attribute to directly measure in the field, photogrammetric techniques allow indirect estimation of body mass and has been used in many cetacean and pinniped species to make indirect measurements of animal morphometrics (Cubbage and Calambokids 1987, Best and Ruther 1992, Castellini and Caulkins 1993, Ratnaswamy and Winn 1993) and to estimate body mass in several large phocid species (northern elephant seals, *Mirounga angustirostris*, Haley *et al.* 1991, southern elephant seals, *Mirounga leonina,* Bell *et al.* 1997, Weddell seals, *Leptonychotes weddellii,* Ireland *et al.* 2006). Photogrammetric mass-estimation techniques are desirable because they are less intrusive than traditional weighing procedures and allow a large number of animals to be sampled. Although a small number of investigators studying large terrestrial mammals have employed photogrammetric techniques to estimate body attributes (*e.g.* bison, *Bison bison*, Berger and Cunningham 1994), marine mammal ecologists are aggressively experimenting and employing the technique for a wide range of species and research questions (Cubbage and Calambokids 1987, Haley *et al.* 1991, Best and Ruther 1992, Castellini and Caulkins 1993,

Ratnaswamy and Winn 1993, Deutsch *et al.* 1994, Haley *et al.* 1994, Bell *et al.* 1997, Engelhard *et al.* 2001, Gordon 2001, Ireland *et al.* 2006).

Photogrammetric mass-estimation techniques first require development of a regression model to predict animal mass from morphometric measurements. Assuming that the model is appropriate for new animals, the regression model is used to predict mass for animals whose mass is unknown, but whose morphometrics are known. Mass predictions can be used: (1) to estimate the mean mass of a population of animals with a given set of morphometrics or (2) to predict the mass of an individual animal with a given set of morphometrics. The expected mass ($E\{Y_h\}$) of the population of animals with a given set of morphometrics (X_h) is the mean of the distribution of Y. When interest is focused on $E\{Y_h\}$, sampling error (variation in the possible location of $E\{Y_h\}$ that is present because the regression coefficients are estimated) must be accounted for in the estimation (Neter *et al.* 1996). In contrast, when predicting mass of a new individual, uncertainty in the predicted mass, referred to as prediction variance, is composed of two sources of variation: (1) sampling error and (2) process variation (variation of the distribution of mass for animals with a given set of morphometrics). Accordingly, the mass of an individual animal with a given set of morphometrics cannot be estimated as precisely as can the mean mass of a population of animals with a given set of morphometrics (Figure 5.1). Further, the uncertainty associated with predicting an animal's mass must be incorporated into subsequent analyses that use predicted mass.

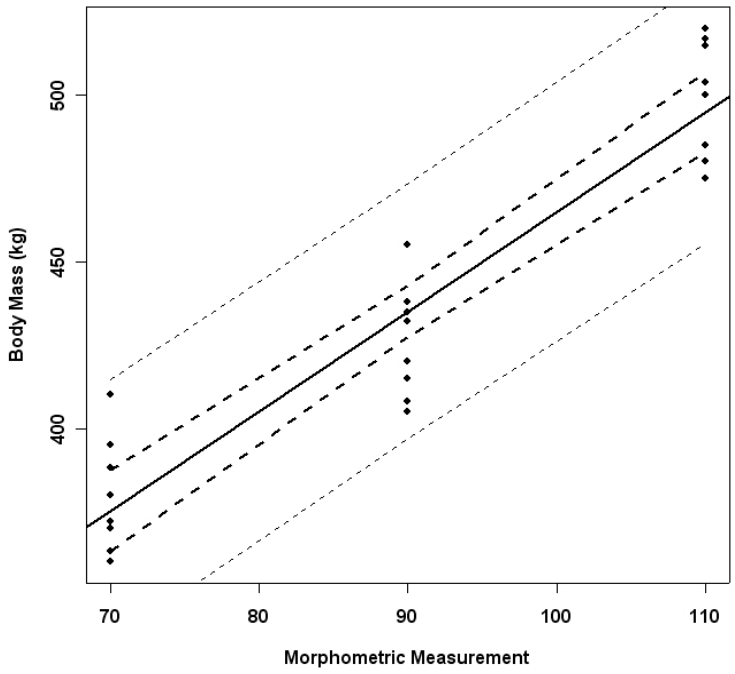


Figure 5.1. The contrast between the confidence interval (inner dashed line), which represents the range in which we are 95% confident the mean mass of animals with a given morphometric measurement is located, and the prediction interval (outer dashed line), which represents the range in which we are 95% confident the mass of a new individual with a given morphometric measurement is located.

Regression modeling is perhaps one of the most common analysis techniques employed to investigate biological questions, and below we provide an example of how predicted masses are used in regression modeling, with a goal of clarifying that predicted mass is now a covariate measured with uncertainty. The goal is to estimate the expected value of Y given X, however in this case X is measured with error so we must estimate the mean of Y with Z. Since Z comes from a linear regression model with additive error and the expected value of Z given X is unbiased for X, our estimate of the mean of Y given Z is a classical error model (Fuller 1987, Buzas et. al. 2003). Uncertainty in the covariate value, commonly referred to as measurement error, has received considerable

attention in biostatistical literature because errors in covariates induce bias in estimated regression coefficients (Jaech 1985, Stephanski 1985, Fuller 1987). Further, the statistical power of studies based on imprecise measurements may be reduced (Cook and Stephanski 1994). Here, we describe measurement error associated with photogrammetric mass-estimation procedures; however, measurement error is also a more general issue that occurs in a variety of investigations, e.g., diet analysis (Santos *et al.* 2001, Boyd 2002). Although multiple error models exist, we focus this paper on the classical error model (see Buzas *et al.* 2003 for discussion of other error models), recognizing the Berkson error model may be relevant in some experimental situations where the explanatory variables are fixed, while their true values vary for each observation (Berkson 1950).

Many investigations of variability in animal mass will likely use measures of mass as explanatory variables to investigate hypotheses of interest. When doing so, researchers must choose between measuring mass directly (time intensive and perhaps impossible depending on species; minimal measurement error) or indirectly (quick and feasible; measurement error involved). To gain insight into the tradeoffs involved when choosing between direct and indirect mass measurements, we used Monte-Carlo simulation techniques to investigate the statistical properties of regression analyses that used direct and predicted mass measurements as explanatory variables. We used simulation techniques because they are illustrative and transparent for identifying bias created by measurement errors and seeing how bias can be corrected. Using data collected from Weddell seals as an example, this paper investigates how prediction variance resulting from estimating animal mass using photogrammetric techniques affects

regression statistics. We first provide an example illustrating that error in a predictor variable induces bias in regression coefficients, then introduce methods that incorporate measurement error and thereby reduce estimation bias, and finally discuss available analysis options for more complex measurement-error scenarios. Through these exercises we demonstrate that understanding prediction variance, and the consequences of prediction variance in applications of photogrammetric methods, is crucial to sampling design, analysis, and interpretation of results. Investigators who have been employing photogrammetric techniques to predict mass have overlooked prediction variance (Deutsch *et al.* 1994, Haley *et al.* 1994, Engelhard *et al.* 2001), and here we demonstrate how appropriate treatment of prediction variance can enhance biological insights by correcting for biases in coefficient estimates. The statistical properties of the scenarios considered in this paper, which are based on data collected from the Weddell seal, are likely representative of analyses applicable to other marine mammal researchers employing photogrammetric mass-estimation techniques.

Methods

Field data from Weddell seals were at the core of our simulation work. Therefore, we first briefly describe the field protocols for directly measuring masses, then the simulation work conducted with these data. We refer the reader to Ireland *et al.* (2006) for additional information regarding development and applications of the mass-estimation model. During the 2004 pupping season, the maternal post-parturition and pup weaning masses of 25 Weddell seal mother-pup pairs were directly measured in Erebus Bay, Antarctica. Maternal post-parturition masses were measured by coercing animals onto a

digital weight platform (Maxey Manufacturing, Fort Collins, CO), and pup weaning masses were measured by rolling pups into a sling and weighing using a spring scale. The animal mass data used in our simulations was generated based on these directly measured mother-pup masses. Using bootstrap sampling, the mean, variance and covariance of maternal post-parturition and pup weaning masses were calculated, and from these calculations we simulated masses of 75 mother-pup pairs (MATLAB, The MathWorks Inc., v6.5). For the purposes of our simulation study, we considered these data as the true maternal and pup masses (measured without errors).

Regression Models and Simulations

To demonstrate the level of bias in estimated regression statistics that result from ignoring measurement error, we developed regression models that regressed pup weaning mass (Y) on maternal parturition mass (X), and we compared the results of analyses employing true mass (measured without error) with those using simulated photogrammetrically predicted mass data (measured with error). Using the linear models function in R (R Development Core Team 2004), we first developed a regression model of pup weaning mass that used the directly measured maternal mass (X) as the explanatory variable, and we considered these regression statistics the true values. Next, we developed a regression model of pup weaning mass that used photogrammatically-estimated maternal masses incorporating prediction variance (X_e, now measured with error) as the explanatory variable, and compared these naïve regression statistics to the true values.

Prediction variance was calculated from photogrammetrically estimating the post-parturition mass of 33 animals (Ireland *et al.*, in press), calculating the mean prediction variance, then introducing the mean variance into each true maternal mass. The variance of each photogrammetrically predicted mass (σ^2_{pred}) was calculated as:

$$\hat{\sigma}^2_{pred} = MSE + \hat{\sigma}^2\{\hat{Y}_h\}, \qquad 1$$

where *MSE* was the mean square error from the mass-estimation model and $\hat{\sigma}^2\{\hat{Y}_h\}$ was the estimated variance of the sampling distribution of predicted mass for a seal with a given set of photogrammetric measurements denoted as X_h (Neter *et al.* 1996). Based on the standard regression assumptions, the prediction error is normally distributed with mean zero and variance given by the prediction variance. We introduced the mean prediction error into each true mass by shifting each mass by a random number of standard prediction errors, where each random deviate was drawn from a normal distribution with mean 0 and variance 1. The new maternal post-parturition mass (that included prediction error) for the ith individual was computed as:

$$X_{e,i} = X_i + \mathrm{RandN}_i * \sqrt{\sigma^2\{\mathrm{pred}\}} \qquad 2$$

where X_i was the true maternal mass and $X_{e\,i}$ was the maternal mass estimated with error.

Bias-Correction Techniques

In the case of simple linear regression, when the explanatory variable has been measured with error, parameter estimates can be bias-corrected using the equations:

$$\beta_{1_c} = \frac{m_{XY}}{(m_{XX} - \sigma_{uu})} \qquad 3$$

$$\beta_0 \cong \overline{Y} - \beta_c \overline{X} \qquad 4$$

$$R^2_c = \frac{mXY^2}{((m_{XX} - \sigma_{uu}) * mYY)} \qquad 5$$

where β_{1c}, $\beta_{0c,}$ and R^2_c are the bias-corrected slope, intercept, and coefficient of determination, m_{XY} is the covariance between the observed X and response Y, m_{XX} is the variance in the observed X's, σ_{uu} is the error variance in the predictor variable X (Fuller 1987).

Using the data described above, we applied bias-correction techniques to the model of pup weaning mass as a function of maternal post-parturition mass, which incorporated prediction errors, and used a simulation approach to estimate β_{1c}, $\beta_{0c,}$ and $R^2_{c.}$ The original dataset (the directly measured masses) was re-sampled using bootstrapping techniques, and 500 sets of 75 true mother-pup masses were generated. For each dataset, the data were first fit to a model regressing pup weaning mass on maternal post-parturition mass, and the true regression statistics were calculated ($\beta_{0T,}$ $\beta_{1T,}$ R^2_T). Next, prediction variance was introduced into maternal mass estimates (Eq. 2), and the naïve ($\beta_{0\,N,}$ $\beta_{1\,N,}$ $R^2_{\,N}$) and bias-corrected regression statistics ($\beta_{0\,c,}$ $\beta_{1\,c,}$ $R^2_{\,c}$) were calculated (Eqs. 3-5). These three sets of regression statistics (true, naïve, and bias-corrected) were estimated for each of the 500 datasets, and the average regression statistics were calculated from the replicates.

Effects of Sample Size

We first explored how the bias in regression statistics was influenced by sample size with a goal of determining if the benefits of increasing sample size using

photogrammetric techniques could overcome the bias resulting from prediction variance in the photogrammetrically estimated masses. We repeated the regression modeling and bias-correction procedures described in the previous section using sample sizes of 10, 25, 50, 75, 100, 150 and 250, and investigated how the magnitude of the bias and bias correction procedure performed as sample size changed. Five hundred datasets at each sample size were generated, and the true, naïve and bias-corrected regression statistics were averaged over all replicates.

We next explored how the magnitude of prediction errors influenced the bias in regression statistics. First, we generated 25 pairs of mother pup masses and incorporated prediction variance in maternal post-parturition mass, using only half of what we calculated to be our prediction variance. Five hundred datasets were then generated, and the averaged true, naïve, and bias-corrected regression statistics were calculated. We repeated these procedures, varying the level of prediction error. We selected levels of prediction errors that would be realistic results of photogrammetric mass estimation procedures (the error observed in our field study was multiplied by 0.5, 1, 1.5, and 2). Finally, we repeated these procedures for sample sizes of 50, 75, 100, and 250 pairs of animals. Five-hundred datasets of each sample size were generated for each of the four levels of prediction error.

Results

When simulated pup weaning masses were regressed onto simulated maternal post-parturition masses that were measured with error, the naïve regression coefficient for maternal mass (β_{1N}) was biased towards zero, and the naïve coefficient of determination

was lower (by 30%) than the true value. The true regression statistics (with standard errors in parentheses) were β_{0T} = -1.32(10.30), β_{1T} = 0.23(0.02), and R_T^2 = 0.58, whereas the naïve regression statistics were β_{0N} = 30.17(10.21), β_{1N} = 0.16(0.02), and R_N^2 = 0.41. In contrast, the bias-corrected regression coefficient approximated the true value and the bias-corrected coefficient of determination was within 2% of the true value. (β_{0C} = -2.70(11.64), β_{1C} = 0.23(0.06), and R_C^2=0.59.

At all sample sizes, the bias-corrected regression coefficients were nearer to the true values than the naïve estimates (Figure 5.2). At the smallest sample size tested, n = 10, a modest amount of bias remained in the bias-corrected value (β_{1T} = 0.23(0.07), β_{1C} = 0.19(0.90)), but it was an improvement over the naïve estimate was (β_{1N} = 0.16(0.07)). At this small sample size, the precision of the bias-correction procedure was low. As sample sizes increased, the bias-corrected estimates approached the true values, whereas the naïve estimates were consistently biased low. At sample sizes of 50 and above, the bias-corrected values approximated the true values very well and the standard error around the coefficient estimate decreased. Given the level of error tested here, the sample size of photogrammetrically estimated masses had to be doubled to obtain the same explanatory power as would have been realized if the maternal masses had been directly measured. The precision of the bias-corrected regression statistics increased as sample size increased, and for this dataset the standard error around the coefficient estimate stabilized at a sample size of approximately 75 (Figure 5.2).

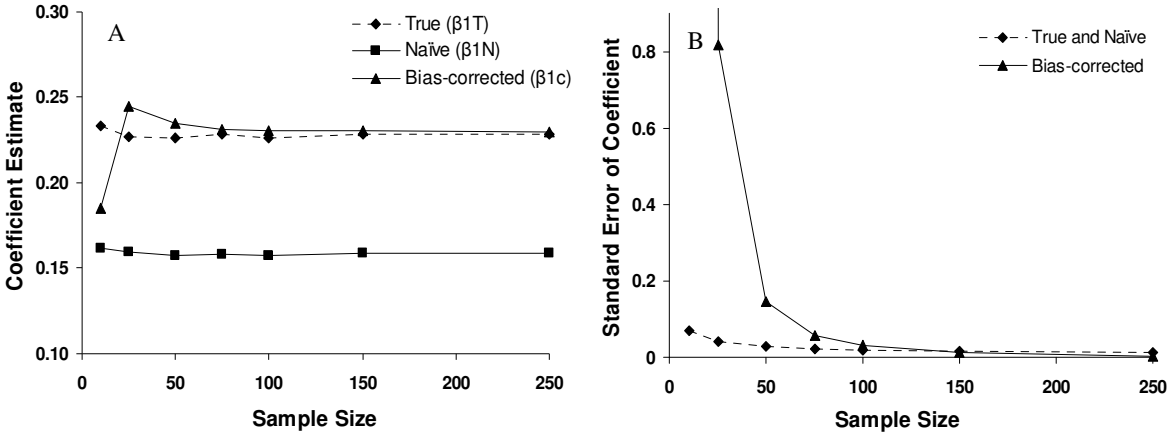


Figure 5.2. The effect of sample size on the regression of pup weaning mass on maternal post parturition mass when the predictor variable maternal mass was directly measured (True), estimated with errors (Naïve), and estimated with errors and corrected for bias (Bias-corrected). Panel A shows the relationship between sample size and the coefficient estimate and panel B shows the relationship between sample size and precision of the coefficient estimate. In panel B, the True and Naïve standard errors were similar and are displayed as one value.

As the magnitude of the measurement error increased, the bias-correction procedure required larger sample sizes to approximate the true regression statistics. The sample size of photogrammetrically estimated masses needed to obtain explanatory power equivalent to that of directly measured masses varied with the level of prediction error. At the original level of error, the bias-corrected regression coefficient approximated the true value at a sample sizes of 50 and above. However, when prediction error was doubled, a minimum sample size of 250 was required for the bias-corrected regression coefficient to approximate the true value (Figure 5.3).

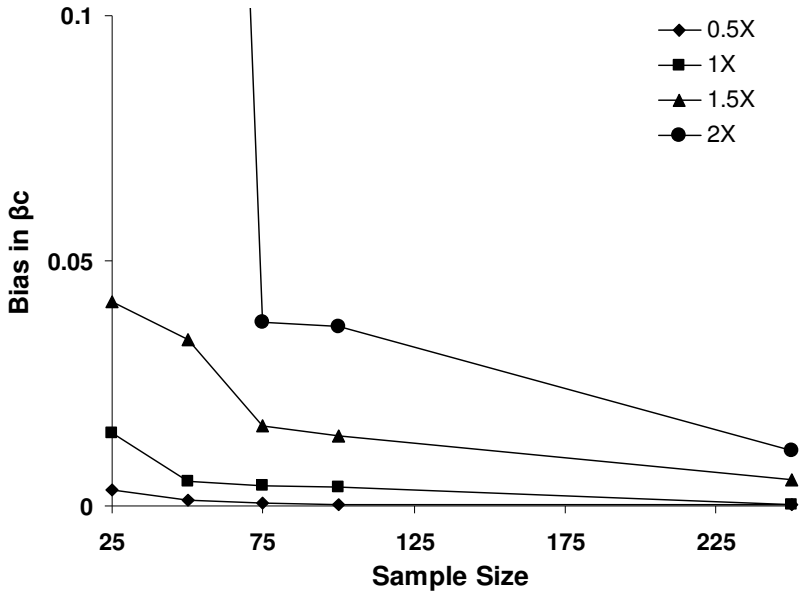


Figure 5.3. The effects of sample size and level of prediction error on the bias in the corrected regression coefficient, calculated as $\beta_{1T} - \beta_{1c}$, for the regression of pup weaning mass on maternal post parturition mass. As the magnitude of prediction error increased, larger sample sizes were necessary for the bias-corrected regression coefficient to approximate the true value.

Discussion

Estimating animal mass using photogrammetric methods is a logistically efficient and non-intrusive data collection technique. However, if mass estimates are to be used as explanatory variables in subsequent analyses, it is imperative that the prediction variance introduced through the mass-estimation procedure be considered and properly accounted for. We have demonstrated that the use of photogrammetrically estimated masses (which include prediction error) as covariates in regression analysis causes the associated regression coefficient to be biased low. It is also important to understand that including a covariate that was measured with error in a multiple regression model not only biases the

regression coefficient for this covariate, but also introduces error into the coefficient estimates for each of the other covariates, even if these other covariates are measured without error (Fuller 1987). Thus, the measurement error introduced when estimated masses are used significantly reduces the explanatory power of a regression model (Cook and Stefanski 1994). In the example provided, modeling pup weaning mass as a function of maternal post-parturition mass, the explanatory power of the naïve regression model was 30% less than the explanatory power of the true and bias-corrected models. The mass-estimation model employed in these analyses had a high coefficient of determination ($r^2 = 0.90$), which is similar to what was found for mass-estimation models that were developed for other species (northern elephant seal, $r^2 = 0.93$-0.95, Haley *et al.* 1991, southern elephant seal, $r^2 = 0.84 – 0.99$, Bell *et al.* 1997). However, even with such high predictive precision, masses estimated from our model, when used as covariates in subsequent modeling, still significantly biased regression coefficients and decreased the explanatory power of the subsequent modeling. We expect researchers employing similar photogrammetric mass-estimation techniques also experience bias and reduced explanatory power if not correcting for prediction error, and the simulation-based framework presented here is an applicable method for exploring prediction variance and trade-offs between sample size and level of precision.

We successfully employed Fuller's (1987) methodology to account for measurement error in our simple linear regression example. However, for more complex situations, alternative methodologies of handling measurement error may be needed. Alternatives include regression calibration, simulation-extrapolation, structural equation modeling, and Bayesian methods (Carroll and Stefanski 1990, Cook and Stefanski 1994,

Maruyama 1998, Congdon 2001). The regression calibration method relates a dependent variable, *Y,* by a regression model to covariate *X*, when *X* is not directly observed, but *W* (*X* with error) is observed in its place. To estimate the regression coefficients, *X* is replaced with an estimate that is a function of *W, X(W)* = E(*X*|*W*) (Carroll and Stefanski 1990, Carroll *et al.* 1995). The simulation-extrapolation method first incrementally adds additional measurement error to the data and iteratively computes the regression statistics; it then fits a model to these estimates and the variance of the added errors and extrapolates back to the case of no measurement error (Cook and Stefanski 1994, Stefanski and Cook 1995, Polzehl and Zwanzig 2004). To use this method, the error variance must be known or at least well estimated. The advantage of simulation-extrapolation is that the method is general, making it useful in applications where the model of interest is novel and conventional methods have not been developed. Structural equation modeling is an extension of the generalized linear model that has more flexible assumptions, and can account for measurement error by having multiple indicators for the latent (true, unobservable variable). Unlike regression analysis, structural equation models test the conceptual and measurement models simultaneously, and measurement errors are identified in the measurement model (Maruyama 1998). The Baysian state-space approach, which models the observation process and the true process of interest simultaneously, can also be applied to measurement error problems (Richardson 2002). Further, Bayesian methods which allow the measurement error to combine classical and Berkson components have recently been developed (Mallick *et al.* 2002). Selection of methodology to incorporate measurement error should depend on the nature of the questions being addressed and the applicability of the various techniques. In this paper,

we used Fuller's (1987) methods because they are straightforward and applicable to the simple linear regression model of interest. When estimated masses are used in more complex calculations, such as to estimate the ratio of pup mass gained to maternal mass loss (mass transfer efficiency) or multiple regression analysis, correcting for measurement error is more complex and novel methods to account for prediction variance must be employed.

Careful sampling design and thorough planning are necessary to effectively utilize estimated masses to address biological questions. First, a thorough understanding of the sources of variance is necessary and allows the investigator to proactively take measures towards reducing this variance. The largest source of prediction variance in the data we utilized was associated with the unexplained variation in the original mass-estimation model (*MSE*). This unexplained variance may be reduced by rigorous standardization of data collection and image analysis protocols. Additionally, increasing sample size of the mass-estimation model and collecting data points at the extremes of the predictive range can further reduce this variance. Second, methods of accounting for prediction variance in estimated masses should be developed when evaluating biological hypotheses that incorporate predicted masses. In regression analysis, failure to account for prediction error in covariates reduces the explanatory power of models and results in biased coefficient estimates. The simple methods described in this paper can correct for this bias. Finally, the precision of photogrammetric techniques must be quantified and considered in defining objectives and sampling protocols. Annual mean parturition or weaning masses can be well-estimated using photogrammetrically estimated masses (Ireland *et al.*, 2006), however using estimated masses with large prediction variances in

individual-based analyses may be more difficult and will likely require at least a doubling of sample sizes for relationships to be detected with the same power that would be realized if direct mass measurements were obtained.

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CHAPTER 6

SYNTHESIS AND DIRECTIONS FOR FUTURE RESEARCH

Synthesis

The long-term Erebus Bay Weddell seal studies have provided a powerful foundation for understanding the population dynamics of a long-lived top-trophic predator. Recently, rigorous analysis of long-term mark resighting data revealed remarkable variations in Weddell seal life history traits and individual reproductive performance, however the mechanisms responsible for these variations were unknown (Hadley 2006). Building upon these long-term studies, we have investigated environmental variability and maternal traits as factors potentially affecting Weddell seal body mass, and we investigated body mass as a factor potentially affecting juvenile survival. The work presented in this dissertation offers novel contributions towards understanding body mass as a mechanism potentially linking large-scale atmospheric-oceanographic processes and reproductive performance. We also identify maternal traits which potentially affect reproductive performance through their affects on body mass.

In Chapter 2, we evaluated variations in maternal body mass at parturition, with goals of relating age-specific variations in body mass with age-specific patterns of reproductive performance and identifying potential linkages between environmental variability and maternal body mass. We hypothesized that maternal body mass at parturition may be a mechanism linking maternal age with reproductive performance, and predicted that age-specific variations in body mass may be consistent with age-specific

variations in offspring survival probability (Hadley *et al.* 2007). Further, we predicted that variability in sea-ice extent and the Southern Oscillation may affect the Ross Sea food web and the foraging success of pregnant seals, resulting in variations in maternal body mass at parturition. We found body mass initially increased with age, reached a maximum at intermediate age, and then showed senescent declines at the oldest ages. Patterns of age-specific variations in body mass were consistent with age-specific patterns of offspring survival probability, supporting our hypothesis that body mass may be a mechanism linking maternal age and reproductive performance. Additionally, body mass at parturition was strongly influenced by environmental variations during the pregnancy period. Specifically, we found an inverse relationship between body mass and summer sea-ice extent and a positive relationship between body mass and the state of the Southern Oscillation. These results suggest that environmental conditions during pregnancy may affect maternal foraging success and may be an important component of Weddell seal reproductive performance.

We continued to explore linkages between large-scale atmospheric-oceanographic variations and Weddell seal body mass in Chapter 3, focusing on annual variations in pup body mass at weaning. We investigated relationships between the annual population average pup weaning masses and summer and winter variations in sea-ice extent, the Southern Oscillation, and the Southern Annular Mode. We found high variability in annual pup weaning masses. Variation in summer Southern Oscillation and summer sea-ice conditions showed the strongest relationship with annual variations in pup weaning mass, and weaning masses were highest following pregnancy periods characterized by low sea-ice extent and strong positive phases of the Southern Oscillation. These results

are consistent with relationships between maternal body mass and environmental variations (Chapter 2), and provide evidence that environmental variations not only affect maternal body mass at parturition, but also may affect maternal energetic expenditure during lactation and consequently offspring body mass at weaning.

In Chapter 4, we investigated relationships between pup body mass at weaning and juvenile survival rates. We estimated age-specific apparent survival rates, and investigated potential relationships between body mass at weaning and apparent juvenile survival rate (survival from weaning to age 3). Mark-resighting models revealed positive relationships between body mass at weaning and apparent juvenile survival rate, and this relationship was considerably stronger in males than females. These results indicate that energy transferred from mother to pup during lactation is important in determining offspring survival rate, and links energetic investment during lactation with a female's fitness. Further, these results suggest that maternal traits and environmental variations that affect maternal body mass at parturition and the magnitude of energy delivered to offspring during lactation likely have important consequences on offspring survival rate, individual fitness, and population dynamics.

Although maternal body mass at parturition has been identified as a key determinant of energetic expenditure during lactation and post-partum reproductive performance (Arnbom *et al.* 1997, Crocker *et al.* 2001, Wheately *et al.* 2006), it is a difficult trait to directly measure in the field. Several studies have explored photogrammetric mass-estimation as an alternative to directly collecting body mass measurements (Haley *et al.* 1991, Bell *et al.* 1997, Ireland *et al.* 2006); however, estimated masses include prediction variance. In Chapter 5, we demonstrated that error

in a predictor variable (such as estimated body mass) induces bias in regression coefficients and described methods that incorporate measurement error and thereby reduce estimation bias. Statistical methodologies such as those described in Chapter 5 may allow future studies to employ photogrammetrically estimated body masses as covariates in ecological modeling exercises. Understanding prediction variance, and the consequences of prediction variance in applications of photogrammetric methods, is crucial to sampling design, analysis, and interpretation of results and we anticipate that these methodologies will increase applicability of photogrammetric mass-estimation in future Weddell seal studies.

Together, our results provide strong evidence that environmental variations influencing prey distribution and abundance may, through their affects on maternal body mass, impact maternal reproductive performance and the dynamics of populations. Environmental variations may affect maternal body mass at parturition (Chapter 2), and through its effects on maternal body mass, environmental variations may affect maternal energetic expenditure during lactation (Wheatley *et al.* 2006), offspring weaning mass (Chapter 3), and ultimately offspring survival rates (Chapter 4). Additionally, the increases in maternal body mass through the young and prime age classes may be a factor leading to age-related increases in offspring survival probability (Hadley *et al.* 2007) and the similar age-related patterns of variations in maternal body mass and offspring survival probability provide additional evidence that body mass is an important component of Weddell seal reproductive performance.

Directions for Future Research

Building upon the long-term demographic and mass dynamics studies will likely reveal new insights regarding relationships between body mass and life history traits, as well as linkages between physical and biological processes. The opportunities for future mass dynamics studies are abundant. As the body mass database continues to grow and animals sampled as pups return as breeding adults, there will be numerous opportunities to investigate relationships between offspring birth and weaning mass and life history traits (specifically age of first reproduction, maternal body mass, and juvenile survival rate), as well as to investigate if variations in growth and body size in early life are propagated throughout an animals life span. Although we have evidence that offspring size at weaning is related to juvenile survival probability (Chapter 4), we presently lack adequate sample sizes to evaluate year effects, and as more data are collected, the analysis in Chapter 4 should be repeated with a year covariate included. Additionally, we describe two potential directions for future research aimed at clarifying relationships between maternal quality and maternal body mass.

Recent Weddell seal studies found that age at first parturition is highly variable and females first reproducing at younger ages may be higher quality individuals than females that delay reproduction until later in life (Hadley *et al.* 2006). Here, we describe a potential future study investigating two contrasting hypotheses related to body mass that may explain variations in age at first reproduction. First, we hypothesize that higher quality females may reach a higher body mass at an earlier age than lower quality

females (Body mass hypothesis). This hypothesis predicts that higher quality females reach a critical body mass necessary for reproduction at an earlier age than lower quality females, and that females of any age will be of similar body mass at first reproduction. Alternately, we hypothesize that higher quality females may have similar age-specific body mass to lower quality females (Efficiency hypothesis). The efficiency hypothesis predicts that females of all quality may be of similar age-specific body mass, and higher quality females may be capable of reproducing at a younger age and lower body mass than lower quality females because they are more efficient during lactation. If there exists variation in mass transfer efficiency during lactation, higher quality females may first reproduce at a younger age than their counterparts of similar age and body mass, and potentially wean offspring that are relatively larger than their counterparts of a similar size but lower quality.

To investigate body mass and efficiency hypotheses, field teams should target first time mothers in their parturition mass sampling. Models explaining variations in body mass at first parturition could be developed, and maternal age and annual environmental covariates could be used to express hypotheses. If there are small annual sample sizes, the population average parturition mass could be used as a more parsimonious covariate representing environmental conditions instead of multiple environmental covariates. The body mass hypothesis predicts that animals of any age first reproduce upon reaching a critical body mass and there is no relationship between body mass at first reproduction and maternal age (Figure 6.1.A). This result would suggest that higher quality individuals capable of reproducing at the youngest ages (Hadley *et al.* 2006) are either genetically predisposed for larger body sizes or may be

superior foragers and attain this critical body mass at a younger age than their inferior counterparts. Alternately, a positive relationship between body mass at first parturition and maternal age provides evidence for the efficiency hypothesis (Figure 6.1.B). This result would suggest animals do not first reproduce at a critical body mass, and that variations in individual traits determining when a female is capable of beginning reproduction are not associated with body mass.

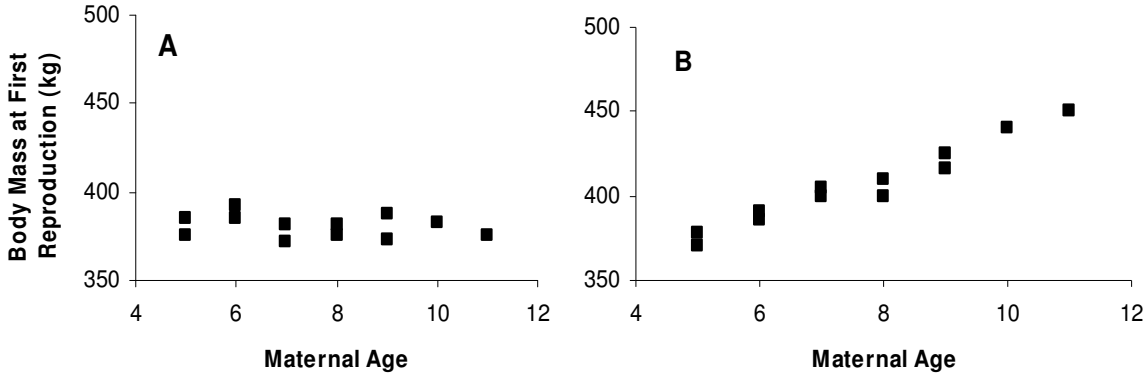


Figure 6.1 Panel A shows the relationship between maternal age at first reproduction and body mass predicted by the body mass hypothesis. The body mass hypothesis predicts that females first reproduce at a given body mass, regardless of maternal age and supports the idea that higher quality females reach a critical body mass at younger ages than lower quality females. Panel B shows the relationship between maternal age at first reproduction and body mass predicted by the efficiency hypothesis. The efficiency hypothesis predicts that females of all quality have similar age-specific body mass, but those females of higher individual quality are capable of sustaining pregnancy and lactation at a lower body mass. The positive relationship between age at first reproduction and body mass indicates that animals do not first reproduce upon attaining a critical body mass and suggests that higher quality individuals are capable of reproducing at lower body masses than lower quality individuals.

Follow-up studies could focus on linking variations in body mass or fat metabolism with genetic variations. Previous studies have demonstrated that genomic diversity is correlated with body mass at birth (Coltman *et al.* 1998, Coulson *et al.* 1998) and if the body mass hypothesis is supported, future studies could investigate

relationships between genomic diversity and Weddell seal body mass. If genomic diversity and body mass are related, increased body mass may be a mechanism by which genomic diversity increases maternal reproductive performance and fitness. If data support the efficiency hypothesis, genetic studies could focus on identifying variations in genes coding for fat metabolism and correlating these variations with variations in age at first reproduction.

If the efficiency hypothesis is supported, follow-up studies should focus on investigating environmental variations and maternal traits potentially affecting mass transfer efficiency. Previous studies have reported high individual variations in mass transfer efficiency (Hill 1987, Wheatley *et al.* 2006), however no studies have investigated how variations in transfer efficiency relate to variations in maternal traits or environmental conditions. Variations in transfer efficiency may produce variations in the costs of reproduction, and high quality individuals may reduce the costs of reproduction by 1) having lower maintenance costs during reproduction, 2) producing offspring that assimilate a higher proportion of mass transferred, or 3) more efficiently converting stored fat resources to milk. Mass transfer efficiency may also be a useful metric of individual maternal quality, and could be used as a covariate explaining variations in offspring growth rates and weaning mass. The data to evaluate variations in mass transfer efficiency are currently available for approximately 125 mother-pup pairs measured during five different years.

Another direction for future mass dynamics studies is to investigate variations in individual's body mass and reproductive expenditure over the course of their reproductive lifespan. Longitudinal sampling may provide additional and more

convincing evidence of senescent declines in maternal body mass (Bowen *et al.* 2006) and monitoring individuals over time may provide new insights into relationships between body mass and individual quality. One could hypothesize that higher quality females consistently 1) have a higher age-specific body mass, 2) raise offspring with higher growth rates, and/or 3) raise offspring with higher weaning mass than their lower quality counterparts. Additionally, one could hypothesize that these effects would be more pronounced during years when prey resources are poor and the population average parturition mass is low. Investigating these effects may also clarify if higher quality individuals have higher body mass and/or if they are relatively more efficient during lactation than their lower quality counterparts. To pursue this line of investigation, a set of easily accessible females (i.e. animals showing fidelity to Razorback or Turks Head) should be selected and targeted for mass sampling each year they reproduce in Erebus Bay.

The long-term Weddell seal studies have established that there are large variations in maternal life history traits and reproductive performance (Hadley 2006), and the work in this dissertation shows that there are large variations in body mass linked to both environmental variations and reproductive performance. However, additional studies are needed to clarify how variations in body mass are linked with variations in individual quality, genetic variations, and reproductive performance. Maintaining intensive mass dynamics studies over a longer time period may improve our understanding of relationships between environmental variations and body mass, and as additional metrics of environmental variability become available (estimates of primary production, sea-

surface height, etc.) new insights into linkages between large-scale atmospheric-oceanographic variations and population dynamics may be revealed.

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