

MASS ESTIMATION OF WEDDELL SEALS  
THROUGH PHOTOGRAMMETRY

by

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## ABSTRACT

Food resources of pelagic marine predators have traditionally been difficult to monitor and annual monitoring of food-resource availability is not currently feasible for the Weddell seal (*Leptonychotes wedellii*) population in Erebus Bay, Antarctica. Body mass measurements of parturient females, or their weaned pups, on an annual basis may be used as an indicator of food availability during the previous year and also provide a link between population vital rates and environmental fluctuation. Traditional methods of acquiring mass measurements, including physical restraint and/or chemical immobilization, limit the ability to sample adequately large numbers of individuals from the population of interest. Previous researchers have developed methods to estimate the mass of large seals using scaled photographs, but later application of these methods have not explicitly included uncertainty around estimates derived from predictive equations. I therefore developed the equipment and methods for estimating the mass of Weddell seals using digital photographs and image-analysis software. I then applied the method at a small scale to determine how prediction intervals may be incorporated into calculations based on mass estimates and what affect the explicit use of these intervals would have on the ability to detect differences between the mass of individuals or groups of seals. Scaled photographs of adult female and pup Weddell seals were taken from overhead, ground-level side, and ground-level head or tail perspectives. Morphometric measurements from scaled photographs (photogrammetric measurements) were then correlated using regression against the measured mass at the time of photography. Sampling occurred throughout the nursing period in order to build regression models over a wide range of masses. Resulting regression models predict the mass of adult female seals to within  $\pm 13.8\%$  of estimated mass, and  $\pm 25.9\%$  of estimated mass for pups. In an application of the method, differences in mass transfer between experienced and inexperienced maternal females and their pups were detected when prediction intervals were explicitly included. Detection of differences between individual seals may not be possible when prediction intervals are included with mass estimates, but estimated mass measurements should be useful for comparing mean differences across a population between years in relation to environmental variation.

## INTRODUCTION

Estimating and predicting the effects of environmental fluctuation on biotic populations has become a significant theme in ecological research. In the Southern Ocean, recent studies have considered the response of basal food resources like Antarctic krill (*Euphausia superba*) to large-scale environmental patterns and climate stochasticity (Hunt et al. 2001, Loeb et al. 1997, Siegel and Loeb 1995, Brierley et al. 2002, Priddle et al. 1988). Near the top of the Antarctic marine food chain, response to climatic variation through changes in food availability has been suggested in flying seabirds, penguins, and seals (Jenouvrier et al. 2003, Thompson and Ollason 2001, Croxall et al. 2002, Weimerskirch et al. 2003, Guinet et al. 1994, Testa et al. 1991). These correlations may be indications of forthcoming ecosystem changes if warming trends around Antarctica continue or commercial fishing in the Southern Ocean increases. Identification of the links between environmental variation and top predators through food resource fluctuations may provide a more complete picture of how Antarctic marine populations will react to a changing environment.

Population trends are rooted in the response of individuals to the prevailing local and regional conditions including food availability. In terrestrial animals it has been documented that a reduction in per capita availability of food resources, either due to climate or density dependence, leads to a decrease in body condition of individuals, which in turn affects fecundity rates and age of maturity (Gaillard et al. 2000, Sæther 1997). However, food resources of marine predators have traditionally been very difficult to monitor. Studies on pinnipeds have found a correlation between maternal

parturition weight, which is likely affected by food availability, and the pup's rate of mass gain and/or weaning mass (Crocker et al. 2001, Mellish et al. 1999, Iverson et al. 1993, Anderson and Fedak 1987, Bowen et al. 1987, Kovacs and Lavigne 1992, Le Boeuf et al. 1989). However, these studies were primarily focused on documenting the length, duration, and intensity of the nursing period exhibited by the various species. Because most investigators were not working with well-marked populations, the effects of variation in adult female mass on pup survival and eventual recruitment were not documented. Two notable exceptions to this involve Hawaiian monk seals (*Monachus schauinslandi*) and northern fur seals (*Callorhinus ursinus*), where a positive correlation between pup weaning mass and survival has been documented (Craig and Ragen 1999, Baker and Fowler 1992). Systematic collection of population wide maternal parturition mass or post-weaning pup mass, in conjunction with long-term population and environmental data, may provide a better understanding of the effects of environmental fluctuation and changes in food availability on pinniped populations.

Extensive population data on the Weddell seals (*Leptonychotes weddellii*) occupying Erebus Bay, Antarctica has been collected since 1968 using mark-recapture techniques (Testa and Siniff 1987), making this population an ideal candidate for the establishment of a mass measurement program. Through the annual tagging effort, much of the population is marked and of known age, allowing long term population trends to be documented, including a relatively constant adult population size since 1978, with cyclical changes in reproductive rates (Testa 1986, Cameron 2001). These cycles in reproductive rate appear to have a delayed, but close relationship to patterns seen in the Southern Oscillation Index (SOI) (Testa et al. 1991). Establishment of a mass

measurement program along with the ongoing population research could elucidate the pathway between environmental variation and population vital rates.

Mass measurements on adult and pup Weddell seals have been collected during numerous studies over the past thirty years (Castellini and Kooyman 1990, Ponganis et al. 1993, Castellini et al. 1988, Braun-Hill 1987, Tedman and Green 1987, Tedman and Bryden 1979). However, the accuracy of mass measurements needed for these physiological studies have required laborious and time consuming techniques including the use of immobilizing agents and subsequent suspension from a portable tripod, or herding non-sedated animals onto a platform scale mounted on skis. Utilization of accurate, but time-consuming techniques has led to small sample sizes over short times spans resulting in limited application to population-wide questions. Application of these mass measurement methods at a population-wide scale could be highly disruptive to the animals and difficult to implement.

Exploring an alternative to collecting actual mass measurements, Castellini and Kooyman (1990) took morphometric measurements of standard length and axillary girth while animals were sedated. They correlated these measurements with the measured weight of the animal to produce relatively accurate predictive equations of mass. In fact, similar models have been produced for a large number of both Arctic and Antarctic seals (Laws 1993, Scheffer 1967). Although use of morphometric measurements to gather mass information does not require the use of a platform or hanging scale, collecting these measurements in an accurate manner still requires physical restraint, if not chemical immobilization. A more efficient and less disruptive technique for gathering mass information is necessary in order to be applied at a population-wide scale.

Morphometric measurements from scaled photographs (photogrammetric measurements) have been successfully used to produce mass estimation equations for northern elephant seals (*Mirounga angustirostris*) and southern elephant seals (*Mirounga leonine*) (Haley et al. 1991, Modig 1995, Bell et al. 1997) similar to those obtained from direct physical measurements (Castellini and Kooyman 1990, Laws 1993, Scheffer 1967). This method for estimating mass from photographs has the potential to be both less disturbing to subjects, and efficiently applied to a large number of seals. The best estimation techniques and models will minimize the uncertainty surrounding individual mass estimates. That is, they will have the narrowest prediction intervals surrounding the model (Neter et al. 1996). For example, both Haley et al 1991 and Bell et al 1997 used the narrowest prediction intervals criterion to select their best mass estimation models, although the methods of interval calculation differed between the two studies. Once techniques and models of mass estimation are developed, the application of the method may proceed. Uncertainty around individual mass estimates should then be expressly incorporated when observations are used to address ecological questions. Depending on the precision of the estimation model, prediction intervals may be quite large and therefore require large sample sizes. A full exploration of the value of a mass estimation technique must consider the utility of the estimates when the uncertainty surrounding each estimate is explicitly dealt with.

Previous photogrammetric mass estimation models have been developed under certain limitations which must be addressed before wide scale application of this technique is practical on the Erebus Bay Weddell seal population. For example, subjects photographed by Bell et al. (1997) were immobilized for other purposes and placed into

very consistent body positions at the time of photography. Future use of these equations would therefore require identical body positions which may only be achieved through immobilization, something I want to avoid. Similarly, only the less aggressive, male northern elephant seals were photographed by Haley et al. (1991) because they were able to be approached and body positions could more easily be standardized. Also, the set of observations from which the final models were derived contained repeated samples from the same individuals. For this method to gather enough useful mass information to relate to Weddell seal population vital rates, it must be applied to, and therefore developed upon, non-sedated adult females and pups. Additionally, predictive equations must be built upon independent observations of mothers and their pups that cover the widest possible range of masses.

My primary objective was to develop and assess the accuracy of separate predictive equations for estimating the mass of non-sedated adult female and pup Weddell seals using measurements from scaled photographs. In order to accomplish this, I needed to design the equipment and identify techniques to efficiently photograph non-sedated seals. For the models to be as precise as possible, I also needed to develop an efficient and repeatable method for obtaining measurements of body morphometrics from digital photographs using image-analysis software. Additionally, both the photographic and image analysis methods needed to be developed in such a way as to allow a large number of mass estimates from throughout the population to be gathered on an annual basis and analyzed in a timely manner. My second objective was to then apply these techniques in a pilot study to demonstrate the utility and limitations of the technique and resulting mass estimates for addressing biological questions.

## STUDY SYSTEM

Research was conducted on the Erebus Bay Weddell seal population in McMurdo Sound, Antarctica (77°43'S x 166°30'E). During the breeding season (mid October through mid December) the Bay is covered by annual or multi-year fast ice, at least 1-2 meters thick, which forms each winter. The region of fast ice along the southwest side of Ross Island contains 13-15 annually occurring tidal cracks that are utilized by adult female Weddell seals to haul out, give birth, and nurse pups (Stirling 1969, Kooyman 1981). These cracks in the sea ice form along five nearshore islands and a number of points of land. As a result of current ice conditions and due to the necessity of towing a weigh sled near to the animals, seals from Big Razorback Island, Little Razorback Island, Tent Island, and Turks Head colonies were used in this study. Since 1973, newborn Weddell seal pups have been tagged in the inter-digital webbing of each rear flipper with individually-numbered livestock tags. Tags have been replaced as needed to maintain a sample of known-aged animals. At this time, approximately 90% of the Erebus Bay population is marked and 74% of the population was initially tagged as pups and are, therefore, of known age (unpublished data).

## METHODS

### Photograph Acquisition and Mass Measurements

Photographs of post-parturition females and pups were collected from three perspectives: overhead, ground level side (side), and ground level head or tail (end). To acquire the overhead perspective photographs, a boom system was built on which a digital camera was mounted and remotely operated by the wearer of the boom. The camera and its protective housing were mounted facing toward the ground on a two-meter pole made of polyurethane coated aluminum tubing (Fig. 1a). The pole was secured to the waist belt and shoulder straps of a backpack which also carried a 12-volt, gel-cell battery that powered the system components. At the lower end of the pole, at chest height on the wearer, were mounted an LCD screen and a housing containing the camera remote control. The LCD screen was linked to the camera viewfinder to allow the seals to be properly framed in the image, and the camera remote housing allowed the zoom in, zoom out, and shutter release to be operated while wearing bulky gloves. A second boom was designed using the same components, but was constructed so the camera was mounted parallel with the ice surface and held approximately 50 cm above the surface of the sea ice (Fig. 1b).

Adult females and pups were photographed separately using Nikon 885, 3.2 megapixel digital cameras at a resolution of 2048 x 1536 pixels. A pole with 20 cm increments marked in alternating colors was held by an assistant in each image so measurements could be calibrated in later image analysis (Figs. 2 and 3).

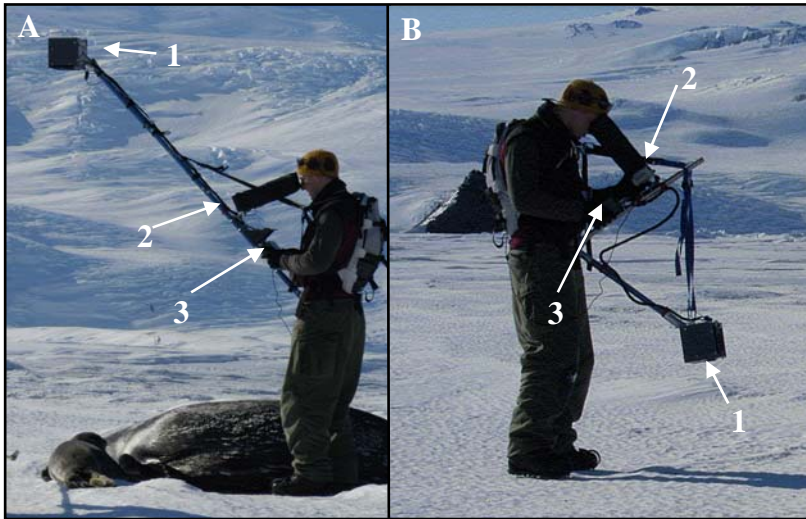


Figure 1. Camera systems used to collect photographs from adult female and pup Weddell seals from the overhead perspective (A) and ground level side and end perspectives (B). The camera housing (1), LCD screen with attached hood (2), and camera remote control (3), are labeled on each camera system.

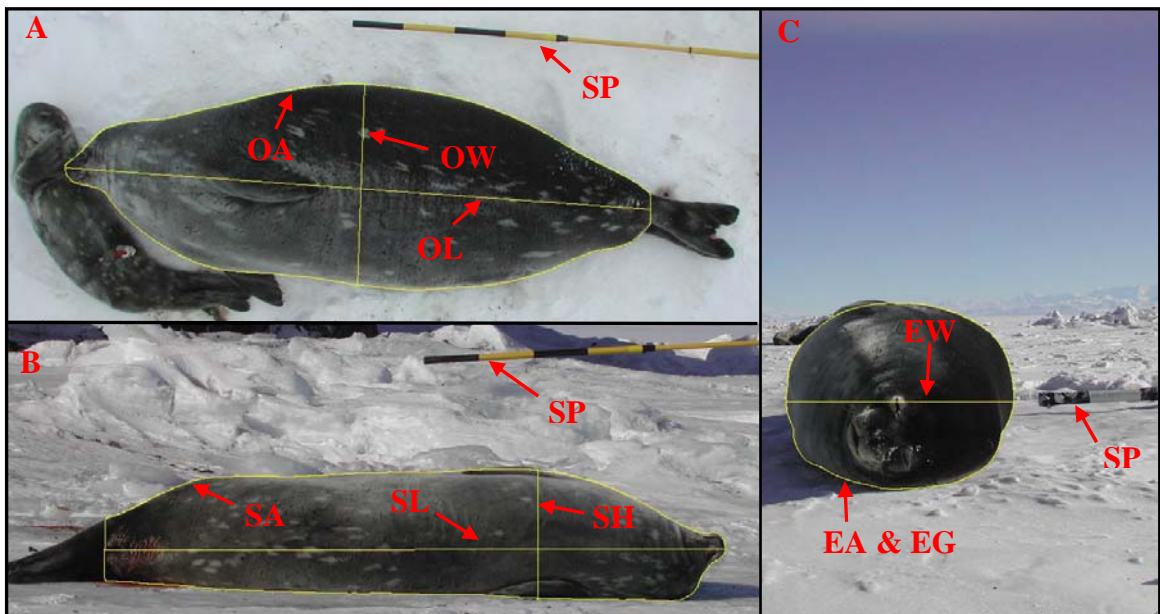


Figure 2. Images of adult Weddell seals exhibiting typical body and head positions, and sea ice surface conditions from overhead (A), side (B), and end (C) perspectives. The scaling pole (SP) is shown in the proper position in each photograph as described in the text. The following measurements are labeled on their respective photographs: overhead area (OA), overhead length (OL), overhead width (OW), side area (SA), side length (SL), side height (SH), end area (EA), end girth (EG), and end width (EW).

In overhead photographs, the pole was positioned parallel to the long axis of the body just above the ground at the seal's greatest width (Fig. 2a and Fig. 3a). For side photographs, the pole was positioned above the midline of the animal, parallel to the long axis of the body, while the photographer stood approximately 2 m from the animal's side at the midpoint of its length (Fig. 2b and Fig. 3b). For end photographs, the pole was positioned perpendicular to the long axis of the body at the point of maximum girth, usually just posterior to the axilla (Fig. 2c). If animals were on rough ice or in depressions melted in the ice by their body heat, they were coaxed to locations of smoother ice before being photographed. Three to five images of each seal from each perspective were taken in order to capture the seal in a standard position in at least one photograph. Pups less than two weeks old were only photographed from the overhead perspective as they had very little height above the surface of the sea ice that could be captured by ground level photographs. Additionally, pups were never photographed from the end perspective since they were highly mobile and reacted strongly to the presence of the photographer directly in front of or behind them. The frame numbers of the photographs taken of each seal were recorded along with the seal's tag numbers and subsequent measured mass.

Immediately after being photographed, seals were weighed on a mobile livestock platform scale that was pulled near to each mother pup pair (dyad). Pup seals were placed on the platform and the mother frequently followed the pup onto the scale. When necessary, the mother was encouraged to follow the pup onto the scale by walking behind and alongside her. The scales used (first year: San Diego Scale Company model number

HP-4896-2K; second year: Maxey Manufacturing, Fort Collins, CO using Rice Lake Weighing Systems load cells – RL35082) were both accurate to within  $\pm 0.5$  kilograms.

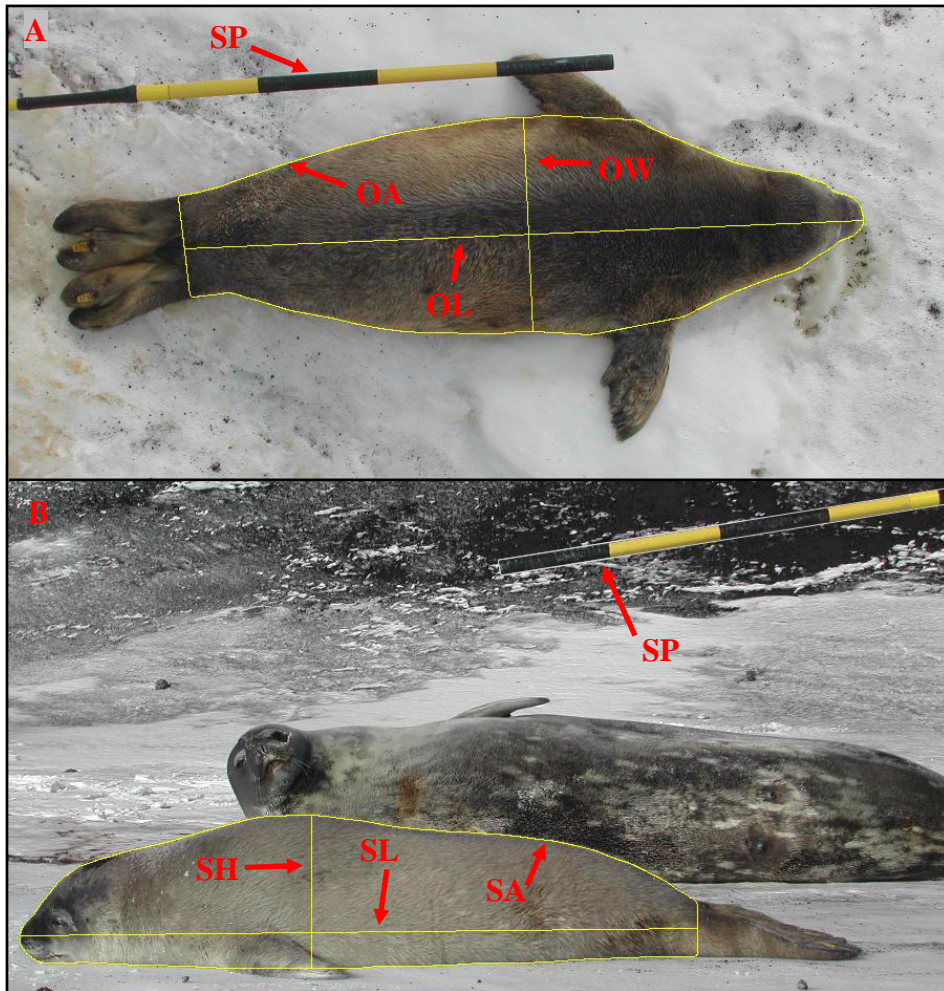


Figure 3. Images of pup Weddell seals exhibiting typical body and head positions, and sea ice surface conditions from overhead (A), and side (B). The scaling pole (SP) is shown in the proper position in each photograph as described in the text. The following measurements are labeled on their respective photographs: overhead area (OA), overhead length (OL), overhead width (OW), side area (SA), side length (SL), and side height (SH).

Photographs and weights of adult females and their pups were collected throughout the nursing period (mid October through mid December) of 2002 and 2003 in

order to capture observations over the broadest possible range of masses. Only tagged seals were photographed and weighed and no seal was sampled more than once during each field season. For the few animals that were weighed once during both seasons, only one of those two mass measurements was used in the final regression analysis. Animals were sampled as dictated by the ability to move the heavy weighing equipment over changing sea ice conditions within Erebus Bay, and the willingness of individual seals to move onto the weighing platform. Colonies at which sampling occurred included Big Razorback Island, Little Razorback Island, Tent Island, and Turks Head.

In 2002, photographs in which both adult female and pup seals were in a variety of body and head positions were taken from each of the three perspectives described above. This was done to determine which head and body positions yielded the most consistent measurements for predicting mass. In 2003, I only took photographs from overhead and ground-level side perspectives and I attempted to take photographs only when seals exhibited standard body and head positions as determined by analysis of 2002 images (described below). Additionally, 10 dyads that were photographed and weighed immediately following parturition were re-photographed at five-day intervals until the mother was no longer seen with the pup, so that mass transfer from females to pups could be evaluated. These 10 pairs were selected to encompass a broad range of adult female parturition weights.

#### Image Categorization and Measurements

Prior to taking measurements from photographs, the body position, head position, and any apparent sea ice surface effects on the seal's outline were categorized as typical,

moderately altered, or significantly altered. The typical position for adults was the position in which most adult females could be found while hauled out nursing pups or sleeping. It also appeared to allow the dimensions of her body to spread out evenly on the surface of the ice. The typical position for adult females can be described as the animal lying on its side such that the visible foreflipper is directly on top of the animal and the snout is pointing straight forwards or relaxed slightly ventrally (Fig. 2). For pups, the typical body position can be described as lying ventrally on the ice with both foreflippers out to each side, and the tail, spine, head, and snout falling along a straight line (Fig. 3). If the head or body was rotated out of these positions or the ice on which the seal was laying was uneven, such that the alterations did not appear to affect measurement accuracy to a significant extent, the observation was categorized as moderately altered. If it was likely that the measurements made on the photograph would be significantly compromised by any or all of the above characteristics being substantially altered from the typical position, then the photograph was categorized as significantly altered. Caudal flippers were not included in any measurements as their shape and position in each photograph were highly variable, so they were not noted during the categorization of images. Image analysis was performed using Image Pro-Express version 4.5.1.3 developed by Media Cybernetics, Inc.

From the set of three to five images taken of each seal from each perspective, the image containing the least sea ice surface effects and the most typical body and head positions was selected. The photograph was ranked as typical, moderately altered, or significantly altered, by the characteristics of the seal and sea ice surface as defined above. For the photograph as a whole to be ranked as typical, the head position, body

position, and sea ice surface effects all had to be ranked as typical. If any one of the three criteria was ranked as moderately altered or significantly altered, then the photograph was ranked at that level. Using the rankings of the photographs associated with each measured weight, each mass observation was placed into one or more of three nested categories. Category three included all mass observations regardless of the ranking of the selected photograph from each perspective, and therefore included all category two and one observations as well. Category two included observations where the selected photographs were categorized as typical or moderately altered, and therefore included all category one observations as well. Category one included observations of mass where selected photographs were ranked only as typical.

Once images were selected and categorized they were opened in the image-analysis software and scaled using the scaling pole that appeared in each photograph. This was accomplished by dragging the software calibration tool over as many entire 20 cm increments of the scaling pole that appeared in the photograph and then entering the total length of those increments. After images were scaled, the following photogrammetric measurements were made on both adult and pup photographs from each perspective. From overhead perspective photographs, three separate measurements were collected (Fig. 2a and Fig. 3a). A two-dimensional surface area measurement (overhead area, OA) was made by tracing the maximum outline of the subject's body, excluding the visible foreflipper if it crossed the outline of the seal, and excluding the caudal flippers by drawing a straight line across the narrowing of the body, just anterior to the caudal flippers at the base of the tail (Fig. 2a and Fig. 3a). Caudal flippers were not included in any measurements and were always excluded as just described. A length measurement

(OL) was made from the midpoint of the cutoff line at the base of the tail to the point of the seal furthest from that point, usually the tip of the nose (Fig. 2a and Fig. 3a). Width measurements (OW) were made by drawing a line perpendicular to the long axis of the body that spanned the maximum width of the seal (Fig. 2a and Fig. 3a). Three separate measurements were also made on side perspective photographs (Fig. 2b and Fig. 3b). A two-dimensional surface area measurement (SA) was made by tracing the maximum outline of the subject's body, excluding the foreflippers and chunks of ice or ice surface irregularities in front of the animal, and excluding the caudal flippers (Fig. 2b and Fig. 3b). A length measurement (SL) was made from the midpoint of the cutoff line at the base of the tail to the point of the seal furthest from that point (Fig. 2b and Fig. 3b). A maximum height measurement (SH) was made from the surface of the ice to the highest point of the seal, usually at or very near to the axilla, excluding the foreflipper (Fig. 2b and Fig. 3b). Three measurements were collected from end perspective photographs, which were only taken for adults in 2002 (Fig. 2c). A two-dimensional surface area measurement (EA) was made by tracing the maximum outline of the body, excluding the foreflippers, as they frequently extended beyond the outline of the body (Fig. 2c). The length of this same line was used as a girth measurement (EG, Fig. 2c). A width measurement (EW) was made by drawing a line parallel to the ice surface that spanned the maximum width of the subject (Fig. 2c).

#### Photogrammetric Precision

Five repetitions of calibration and measurement were made on each of a randomly selected subset of 10 images of adult seals from each perspective (30 total images). In

order to determine the precision of the measurements, the intra-image coefficient of variation ( $s / \bar{x} * 100\%$ ) within each measurement from each image was calculated, and also averaged over each perspective and across all measurements. All statistical analysis was performed using the R statistical analysis software package (Team 2004).

To consider the minimum sampling error between different images of the same seal, ten sets of images of adult seals (3-6 images per set) from each perspective were selected that contained identical looking images of the same seal taken within a few seconds of each other, where the head and body position of the seal did not change between photographs. Measurements were then collected from each photograph and the coefficient of variation between like measurements within each set was calculated to determine the amount of sampling error among photographs (inter-image coefficient of variation).

### Regression Models

An all subsets regression procedure was applied separately to adult female and pup observations within each of the three categories described above. The predicted sum of squares (PRESS) was chosen as the criterion for model selection in order to identify the models which best predicted mass at time of photography as a function of associated photogrammetric measurements.

$$\text{PRESS} = \sum_{i=1}^n (Y_i - \hat{Y}_{i(i)})^2$$

PRESS is a measure of how well a model predicts each observed value when that observation is left out of the model as it is fit, and not simply how well a model fits the

data, as is the case for the coefficient of multiple determination ( $r^2$ ). The smaller the PRESS value, the better the model is at predicting the response variable (Neter et al. 1996).

Ninety-five percent confidence intervals around regression models were calculated using the Working Heteroscedasticity multiplier (Neter et al. 1996). However, confidence intervals only express the confidence one has in the location of the actual regression surface in the predictor space. They do not express the confidence one has around the point estimate of a new observation with a given set of predictor values. To express the level of confidence one has around a predicted new observation, prediction intervals, or “wide” confidence intervals, must be calculated. In this case, minimizing the prediction intervals is of greater concern and more relevance than minimizing the confidence intervals. The model with the narrowest prediction interval is what PRESS selects for. Prediction intervals incorporate two variance components; the variance of the distribution of the response at a given level of predictor values; and the variance of the sampling distribution of the estimate of the response at the given level of predictor values. Prediction intervals, therefore, are much wider than confidence intervals. Prediction intervals were calculated as described in Neter et al. (1996) at an  $\alpha$  of 0.05.

In addition to identifying the model with the greatest predictive ability derived from each category of observations, I wished to compare the predictive ability of models between the different categories in order to assess the level of care necessary for photographing seals in similar head and body positions and sea ice surface conditions. However, PRESS values alone cannot be used for such comparisons because they are additive, and thus models derived from larger, inclusive datasets will have higher PRESS

values. By dividing the PRESS value by the total sum of squares (SSTO), a ratio of the amount of prediction error in the model to the total error in the model is created. This ratio can then be used to compare models derived from different sized datasets. Within a given dataset this ratio will produce the same results as comparing only the PRESS values because the SSTO value is the same for all models derived from the same dataset.

Preliminary all-subsets regression was performed on the 2002 adult and pup datasets. The regression procedure was performed independently on the three categories of observations described above. Based upon results from this preliminary analysis, end photographs were not taken during the 2003 season and more seals were photographed in positions ranked as typical during that season. Because the acquisition of overhead images similar to those used in this study are not possible on most other seal species without chemical immobilization, all subsets regression was also performed on measurements from ground level perspectives only (side and end), in order to compare with similar studies (Bell et al. 1997, Haley et al. 1991).

Following the second field season, the same regression procedure was used on the combined adult female observations from 2002 and 2003, but only the six measurements from overhead and side perspectives were used as potential predictors. This regression analysis was again performed independently within the three categories of observations described above.

Because pups less than two weeks old were only photographed from the overhead perspective, two separate analyses were made on combined 2002 and 2003 pup observations. The first analysis included only measurements from the overhead perspective, and therefore it included the entire sample and full range of mass

observations collected on pups. The second analysis used measurements from overhead and side perspectives, which excluded pups less than two weeks old because side photographs of them were not taken; therefore this was a smaller dataset with a narrower range of mass measurements.

Prediction intervals at an alpha level of 0.05 were estimated for the adult female models at the mean value of predictors included in each model. Because the square root of mass was used as the response in pup models, 95% prediction intervals increase with increasing mass when it is back-transformed. Therefore, prediction intervals were calculated at the smallest, mean, and largest value of predictors included in the model, to describe the full range of possible intervals.

#### Application of the Method

To demonstrate an application of the technique, the final models were then used to estimate mass for the ten dyads that were photographed every five days throughout the 2003 nursing period. Note that the parturition weight for these individuals was an actual measured mass that was collected one to two days after parturition. All subsequent masses were estimated using the appropriate estimation model. Weaning date was considered the last day the mother and pup were photographed together and the mother was no longer seen in attendance through the duration of the season. Mass lost by each mother was calculated by subtracting the estimated mass of the mother at weaning from her measured mass at parturition. Mass gained by the pup was calculated by subtracting the pup's measured mass at parturition from the pup's estimated mass at weaning. Mean values of mass lost and gained are reported with 95% prediction intervals. The rate of

mass lost or gained ( $\text{kg day}^{-1}$ ) was calculated by dividing the mass lost or gained by the individual by the number of days between the parturition and weaning dates for that pair. Percent gained or lost was calculated by dividing the kg gained or lost by the parturition mass of the individual. Percent efficiency was estimated by dividing the kg gained by the pup by the kg lost by the mother.

Prediction intervals around mass estimates at weaning were calculated using a variance estimate that included the sum of the variance of the model fit and the variance of the data used to build the model (Neter et al. 1996). The same variance estimate for weaning mass applied to the kg gained or lost calculated using those weaning weight estimates. Prediction intervals around percent efficiencies were estimated through simulation because the ratio of two random normal values is a Cauchy random variable, and therefore has an uncharacterizable distribution (Casella and Berger 2002). Simulations involved drawing 5,000 paired values of mass gained by the pup and mass lost by the mother to create 5,000 efficiency values. Pairs of mass gained and mass lost values were drawn from a bivariate distribution with means at the estimated values of gain and loss for that pair. Variance estimates around the estimated values of mass lost/gained were equal to those used in the calculation of prediction intervals of the weaning mass estimates from the respective adult and pup regression models. A covariance estimate was used and calculated by multiplying the Pearson's product-moment correlation coefficient of the relationship between pup mass gained and maternal mass lost of these ten pairs by the standard deviations of the respective mother and pup mass estimates. The highest and lowest 2.5% of simulated efficiency values were

omitted and the resulting bounds were used as the 95% prediction limits of mass transfer efficiency. This process was repeated for each mother pup pair.

The sample of 10 dyads included three females for which this was their first known pup and the results from these three pairs appeared quite different from the pairs with more experienced adults. Differences in mean parturition mass, weaning mass, and mass lost by adult females; mean parturition mass, weaning mass, and mass gained by pups; and the mean mass transfer efficiency between experienced and inexperienced dyads were tested using the Scheffe multiple comparison procedure with a family confidence  $\alpha$  level of 0.05. Variance estimates around mean values of mass estimates used in t-tests were the sum of the variance of the mean and the sum of the variance estimates around each estimated value divide by the sample size squared.

$$\text{Var}\left(\frac{1}{n} \sum_{i=1}^n Y_i\right) = \frac{1}{n^2} \left( \text{Var} \sum (\hat{Y}_i) + \sum \text{Var}(\epsilon_{p_i}) \right)$$

Finally, two power analyses were performed with  $\alpha = 0.05$  and  $\beta = 0.05$ , to estimate the number of estimated mass observations of adult females at parturition needed to detect a mean difference in parturition mass of 25 kg and 50 kg between years. A variance estimate for this analysis was developed from the estimated mass values of adult females photographed and weighed at parturition. The variance estimate was calculated in the same manner as just described for testing differences between mean values of mass estimates (Neter et al. 1996).

## RESULTS

### Photograph Acquisition and Mass Measurements

A total of 5,698 scaled digital images were acquired over the two field seasons (adult females-3042 images; pups-2656 images). Mass measurements corresponding with a complete set of images were acquired on 98 unique adults ranging from 224 kg to 648 kg in mass, and 137 unique pups ranging from 17 kg to 183 kg in mass. In 2002, sampling occurred between October 23 and December 8, and between October 25 and December 11 in 2003.

Image sets of adults took between 6 and 14 minutes to acquire while 5 to 10 minutes were required to obtain a complete set of photographs from pups. Categorizing, calibrating, measuring, and entering all information for each image required 3 to 5 minutes to complete. With an improved weighing platform design for the second season, the time required to set up the weigh-sled next to each dyad, or group of dyads, was reduced from 10 to 30 minutes, to 4 to 6 minutes. Gathering weights on pups involved little more time than it took to set up the weigh sled. Adult seals required between 5 and 20 minutes to weigh, depending on the disposition of the seal. Moving the weigh-sled from one position to the next usually required 10 to 20 minutes.

### Photogrammetric Precision

The average intra-image coefficient of variation among replicate measurements was 0.40% (App. A, Table 1). The area measurement from the overhead perspective

(OA) was the most repeatable measurement taken, with a coefficient of variation of 0.19%. The measurements of height from the side perspective (SH) had the largest coefficients of variation at 0.66% (App. A, Table 1). The average inter-image coefficient of variation between like measurements taken from multiple images of the same seal at the same time, in which the seal had not changed head or body position, was 1.3% (App. A, Table 2). The length measurement from the side perspective (SL) had the lowest coefficient of variation at 0.83%. The area measurement from the end perspective (EA) had the largest inter-image coefficients of variation, 2.7% (App. A, Table 2).

### Regression Models

Preliminary regression on 2002 adult female category 2 and category 3 observations revealed that measurements from end photographs did not have high predictive ability on their own (PRESS/SSTO ratio  $< 0.44$ ,  $r^2 < 0.65$ ) and added very little predictive power to models including predictors from the other two perspectives. The number of category 1 observations was too small to be useful for analysis. All subsets regression of mass on measurements from only ground-level perspectives showed SA to be the best single predictor (model 1, Table 1). The three predictor model including SH, EG, and EW measurements (model 3, Table 1) resulted in the smallest prediction intervals using only side-and end-perspective photographs.

Table 1. The best regression equations for the estimation of adult female Weddell seal mass, as determined by the smallest PRESS/SSTO ratio, within three different groups of observations; (1) measurements from side and end perspectives only, (2) category 3 observations (all observations), (3) and category 2 observations (photographs in which the head and body position, as well as sea ice surface conditions, were categorized as typical or moderately altered from typical as described in the text). All regression equations significant at  $p < 0.0001$ , 95% prediction intervals are presented at the mean of predictor(s) used in the model. “% Predicted Mass” is the 95% prediction interval expressed as a percentage of the mean fitted mass. Range of mass in models one through four was 227-648 kg, and 224-648 kg for models five through eleven.

<b>Adult Female Mass Estimation Models</b>						
#	Model	n	$\frac{\text{PRESS}}{\text{SSTO}}$	$r^2$	$\pm$ 95% PI Mean of Predictor(s)	% Predicted Mass
Side and End perspectives only (2002 data only)						
1	$M = 15.26 + 0.041(\text{SA})$	32	0.401	0.654	110.83	27.54
2	$M = -330.96 + 4.16(\text{EW}) + 7.43(\text{SH})$	32	0.308	0.753	95.42	23.71
3	$M = -247.49 - 2.11(\text{EG}) + 9.89(\text{EW}) + 6.64(\text{SH})$	32	0.279	0.798	87.92	21.85
4	$M = 125.64 - 1.662(\text{EG}) + 8.639(\text{EW}) - 1.792(\text{SL}) + 0.040(\text{SA})$	32	0.300	0.802	88.77	22.05
Models including category 3 observations						
5	$M = -100.962 + 6.258(\text{OW})$	98	0.297	0.719	82.31	22.62
6	$M = -156.8 + 3.844(\text{OW}) + 0.0265(\text{SA})$	98	0.181	0.833	63.78	17.53
7	$M = -122.8 + 4.071(\text{OW}) - 0.269(\text{OL}) + 0.0274(\text{SA})$	98	0.185	0.834	63.85	17.54
Models including category 2 observations						
8	$M = -71.18 + 0.049(\text{SA})$	73	0.224	0.788	71.14	19.80
9	$M = -176.5 + 3.754(\text{OW}) + 0.029(\text{SA})$	73	0.115	0.897	50.04	13.93
10	$M = -134.1 + 3.635(\text{OW}) + 0.040(\text{SA}) - 2.497(\text{SH})$	73	0.113	0.901	49.43	13.76
11	$M = -83.312 + 3.611(\text{OW}) + 0.0444(\text{SA}) - 0.246(\text{SL}) - 3.236(\text{SH})$	73	0.115	0.901	49.70	13.83

In the combined 2002 and 2003 dataset, for both adults and pups, the category one observations constituted a relatively small dataset and candidate models did not perform significantly better than models derived from category two observations. Additionally, it was deemed unrealistic for future researchers to gather large samples of observations in which seals were photographed only in typical positions from both the overhead and side perspectives. For example, in 2003, 81% (64 of 79) of adult females photographed and weighed were placed into category two, while only 30% (24 of 79) were placed into category one. This was an improvement over 2002 in which only 44% (14 of 32) of adult females photographed and weighed were placed into category two, while 15% (5 of 32) were placed into category one. Therefore, the results from the category one subset are not presented.

Regression diagnostics and Box-Cox procedures on linear models of adult female mass did not suggest the need to transform the response, or any of the predictors. Using category 3 observations the model with the best predictive ability of adult female mass included the OW and SA measurements and had a PRESS/SSTO ratio of 0.18 (model 6, Table 1). From category 2 observations, the model with the best predictive ability of adult female mass and the overall best predictive ability for adults, included the OW, SA, and SH measurements and had a PRESS/SSTO ratio of 0.11 (model 10, Table 1). The 95% confidence interval around model 10 at the mean value of the OW, SA and SH predictors was  $\pm 5.75$  kg or 1.6% of the fitted body mass. The 95% prediction interval at the mean values of OW, SA and SH predictors for model 10 (Table 1) was  $\pm 49.4$  kg, or 13.8% of the fitted body mass (Fig. 4a).

Non-constant variance of the residuals from linear models of pup mass, and Box-Cox procedures on these models, suggested that a square root transformation of the response, pup mass, would better satisfy the assumptions of linear regression and improve model fit. This type of transformation can also be justified because body measurements tend to scale allometrically to body mass (Peters 1983). For those reasons, all pup predictors were regressed against the square root of the observed mass at time of photography.

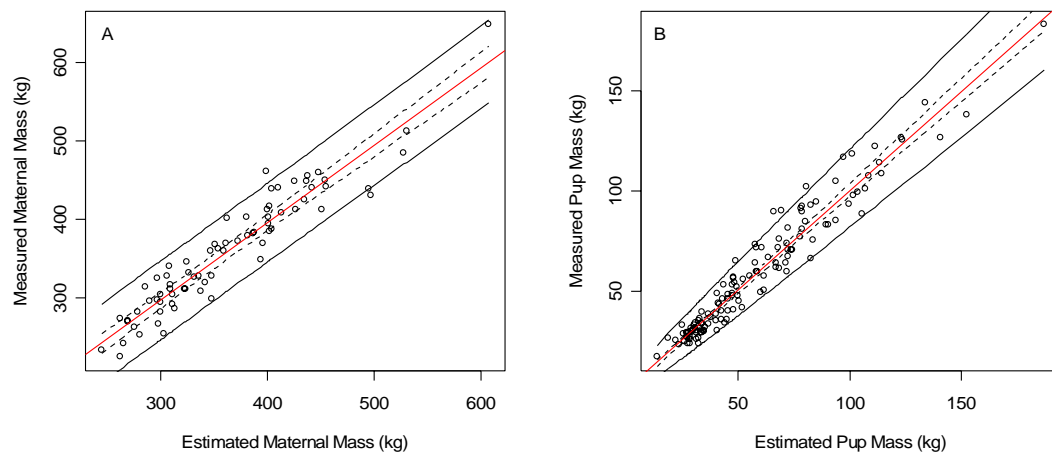


Figure 4. Relationship of the OW, SA, and SH measurements to adult female mass (A)(model 10 Table 1) and the relationship of OW and OA measurements to pup mass (B) after back-transforming the response of  $\text{Pup Mass}^{0.5}$  to Pup Mass (model 16, Table2). Regression models (red lines), with 95% confidence intervals (black dashed lines) and 95% prediction intervals (black solid lines).

Models using measurements from the overhead perspective only performed better than those using both overhead and side perspective measurements. From overhead perspective measurements only, using all observations (category 3), the model with the best predictive ability of pup mass contained the OW and OL measurements and had a PRESS/SSTO ratio of 0.066 (model 13, Table 2). Using the category 2 subset of

observations, the best predictive model, and overall best predictive model of pup mass, included the OW and OA measurements and had a PRESS/SSTO ratio of 0.062 (model 16, Table 2). When the transformed response used in pup models, the square root of pup mass, is back-transformed to actual mass, the 95% prediction intervals expand with increasing predictor values (Fig. 4b, Table 2 for minimum, mean, and maximum prediction intervals). The 95% prediction interval at the mean values of OW and OA predictors for model 16 (Table 2) was  $\pm 14.3$  kg, or 25.9% of the fitted body mass.

Table 2. The best regression equations for the estimation of pup Weddell seal mass, as determined by the smallest PRESS/SSTO ratio, within two categories from two groups of observations. The first group includes mass observations using only overhead perspective photographs and is separated into category 3 observations (all observations), and category 2 observations (photographs in which the head and body position, as well as sea ice surface conditions, were categorized as typical or moderately altered from typical). The second group includes mass observations with overhead and side perspective photographs. All regression equations significant at  $p < 0.0001$ , 95% prediction intervals are presented at the minimum, mean, and max of predictor(s) used in the model. Range of mass in models 12 through 17 was 17-183 kg, and 24-183 kg for models 18 through 24.

<b>Pup Regression Models</b>		n	<u>PRESS</u> SSTO	$r^2$	$\pm$ 95% Prediction Intervals (kg)		
#	Model				Min of Predictor(s)	Mean of Predictor(s)	Max of Predictor(s)
<u>Overhead Perspective Only</u>							
Models including all observations (category 3)							
12	$M^{0.5} = -1.198 + 0.230(\text{OW})$	137	0.069	0.933	7.67	15.3	28.3
13	$M^{0.5} = -2.394 + 0.200(\text{OW}) + 0.0202(\text{OL})$	137	0.066	0.937	7.06	14.8	28.5
14	$M^{0.5} = -1.624 + 0.179(\text{OW}) + 0.0132(\text{OL}) + 0.000246(\text{OA})$	137	0.066	0.938	7.41	14.8	29.3
Models including category 2 observations							
15	$M^{0.5} = -1.198 + 0.230(\text{OW})$	129	0.063	0.938	7.32	14.5	27.0
16	$M^{0.5} = -0.602 + 0.176(\text{OW}) + 0.000417(\text{OA})$	129	0.062	0.941	7.26	14.3	28.5
17	$M^{0.5} = -1.046 + 0.183(\text{OW}) + 0.000314(\text{OA}) + 0.00492(\text{OL})$	129	0.062	0.941	7.40	14.3	28.5
<u>Overhead and Side Perspectives</u>							
Models including all observations (category 3)							
18	$M^{0.5} = -0.539 + 0.217(\text{OW})$	80	0.104	0.900	11.8	17.9	28.4
19	$M^{0.5} = -0.279 + 0.149(\text{OH}) + 0.000795(\text{SA})$	80	0.078	0.928	2.5	15.3	27.0
20	$M^{0.5} = -3.635 + 0.160(\text{OW}) + 0.0204(\text{SL}) + 0.0905(\text{SH})$	80	0.077	0.931	9.0	15.0	25.9
Models including category 2 observations							
21	$M^{0.5} = -0.615 + 0.219(\text{OW})$	70	0.110	0.895	12.1	18.3	20.6
22	$M^{0.5} = -0.224 + 0.141(\text{OW}) + 0.000895(\text{SA})$	70	0.083	0.924	10.1	15.6	28.8
23	$M^{0.5} = -4.0165 + 0.154(\text{OW}) + 0.0235(\text{SL}) + 0.0987(\text{SH})$	70	0.081	0.928	9.3	15.4	26.7
24	$M^{0.5} = -4.572 + 0.139(\text{OW}) + 0.0116(\text{OL}) + 0.0223(\text{SL}) + 0.0228(\text{SH})$	70	0.081	0.930	9.2	15.8	27.6

In comparison, from overhead and side perspectives, the best predictive models had higher PRESS/SSTO values. The best predictive model using category 3 observations included the OW, SL, and SH measurements and had a PRESS/SSTO ratio of 0.077 (model 20, Table 2). Using category 2 observations from overhead and side perspectives, the model with the best predictive ability of pup mass also included OW, SL, and SH measurements and had a PRESS/SSTO ratio of 0.081 (model 23, Table 2).

### Application of the Method

The mean mass at parturition of all 10 adult females photographed throughout the 2003 nursing period was 415 kilograms (Table 3, Fig. 5a). The mean mass of those ten females' pups at weaning was 83.3 kg (Table 3 Fig. 5b). Models 10 (Table 1) and 16 (Table 2) were used to estimate weaning mass for adults and pups, respectively. Adult females lost an average of 135 kg ( $\pm 30.2$ kg,  $n=10$ ) between parturition and weaning while pups gained an average of 51 kg ( $\pm 10.2$ kg,  $n=10$ ). This resulted in a mean mass transfer efficiency of 38% (range 28% - 46%)(App. A Table 4). Duration of the nursing period averaged 34 days ( $n=10$ , range 24-40 days) and the difference between the seven dyads with experienced mothers and the three dyads with inexperienced mothers was large (see Appendix A Figure 1 and Tables 3 and 4 for the mass estimates throughout the nursing period and individual pair mass gained/lost summaries). The mean mass of experienced mothers at parturition was significantly greater than the mean mass of inexperienced mothers (+128.9 kg,  $S = 23.4$ ,  $df = 1$  and 8,  $p = 0.003$ ), and the mean mass of experienced mothers' pups at weaning was significantly greater than the pups of inexperienced mothers (+30.6 kg,  $S = 84.9$ ,  $df = 1$  and 8,  $p < 0.001$ ) (Table 3). Similarly,

the mean mass lost by experienced mothers was significantly greater than the mean mass lost by inexperienced mothers (+69.9kg,  $S = 32.5$ ,  $df = 1$  and  $8$ ,  $p < 0.001$ ), and the mean mass gained by pups of experienced mothers' was significantly greater than that gained by pups of inexperienced mothers' (+27.6 kg,  $S = 61.0$ ,  $df = 1$  and  $8$ ,  $p < 0.001$ ) (Table 3). However, the efficiency of mass transfer only differed by 1.4% between experienced and inexperienced mothers ( $S = 1.13$ ,  $df = 1$  and  $8$ ,  $p > 0.1$ ).

Table 3. Mean parturition and weaning mass from ten dyads photographed throughout the 2003 nursing period. Parturition mass was an actual physical measurement while weaning mass was estimated from photographic measurements using model 10 (Table 1) for adults and model 16 (Table 2) for pups. Prediction intervals are given in kg and apply to both the weaning mass and the mass gained/lost values. Experienced dyads ( $mean_{exp}$ ) were those in which the adult female had at least two previous pups. Inexperienced dyads ( $mean_{inexp}$ ) were those in which this was the first known pup for that adult female. Differences between means ( $mean_{exp} - mean_{inexp}$ ) of parturition mass, weaning mass, and mass gained or lost were tested using t-tests.

		overall mean	$mean_{exp}$	$mean_{inexp}$	difference
Adults	sample size (n)	10	7	3	
	parturition mass	415.1	453.7	324.8	128.9*
	weaning mass	279.8	297.5	238.5	59.0**
	mass lost	135.2	156.2	86.3	69.9**
	± 95% PI (kg)	30.3	30.8	44.9	
	mass lost per day	4.0	4.5	2.9	1.6
	% loss	32.0	34.4	26.6	7.8
Pups	parturition mass	32.2	33.1	30.0	3.1
	weaning mass	83.3	92.6	61.9	30.6**
	mass gained	51.1	59.4	31.9	27.6**
	± 95% PI (kg)	9.7	6.1	4.2	
	mass gained per day	1.5	1.7	1.0	0.6
	% gain	163.5	187.3	108.0	79.3
transfer efficiency (%)		38.0	38.4	37.0	1.4
± 95% PI (%)		3.8	4.5	8.0	

\* $P < 0.05$ , \*\* $P < 0.001$

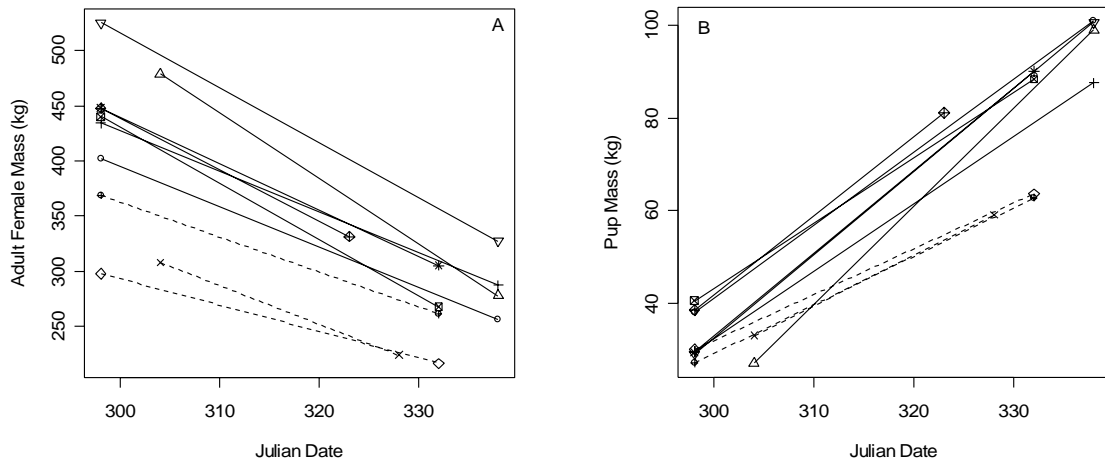


Figure 5. Adult female parturition and weaning mass (A), and pup parturition and weaning mass (B) for ten mother pup pairs photographed throughout the nursing period. Parturition masses were physical measurements while weaning masses were estimated using model 10 (Table 1) for adults, and model 16 (Table 2) for pups. Dashed lines indicate the three dyads for which this was the mother's first known pup.

Power analysis demonstrated that with the variance of 3,960 estimated from all mass estimates of adult females photographed and weighed at parturition,  $\alpha = 0.05$ , and  $\beta = 0.05$ , a sample of approximately 166 individual adult female seals will be needed to detect a difference in mean parturition mass of 25 kg between years. To detect a difference of 50 kg, approximately 42 individuals would need to be sampled at parturition.

## DISCUSSION

The total time necessary to acquire a mass estimate for an adult Weddell seal, including the time required to photograph the seal from two perspectives and to later analyze those images, is between 10-15 minutes. Acquisition of the photographs made up the bulk of this time because care must be taken to acquire photographs when the seal exhibits the proper head and body positions. The duration of time spent photographing each animal varied depending on the disposition of the subject. Many animals remained motionless or even asleep as we photographed them. Other animals moved their head frequently in order to maintain visual contact with both the photographer and the assistant holding the scaling pole. Seals generally reacted most strongly to the approach of the second person and the subsequent positioning of the scaling pole next to them. The most difficult animals reacted very strongly to our presence and a few moved so much that it became apparent we would not be able to acquire photographs of them in the proper positioning, so those animals were not sampled.

Analyzing images took little time and was highly repeatable. The mean and max coefficients of variation for replicate measurements from the same photograph (0.40% and 0.66% respectively) were smaller than the mean and max of 1.4% and 7.8% respectively, reported by (Bell et al. 1997) for southern elephant seals. This improvement is likely a result of using digital cameras and image analysis software that, at times, does not require one to manually digitize outlines. Use of this equipment also eliminates the need to scan pictures, which can cause image distortion. Although image analysis time was not reported in previous studies, automated edge detection tools and the ease of

importing images into the image analysis software have likely reduced the time involved in processing images. The inter-image analysis of photographs with identical head and body positions revealed that the variation between like measurements taken from different photographs was also quite low. This suggests the methods for acquiring body morphometrics from each photographic perspective were repeatable. Because measurements and calibration on the same image were highly repeatable, I chose not to take replicate measurements on each image in order to calculate a mean for use in regression analyses.

Preliminary regression analysis demonstrated that measurements from end photographs were not as useful in predicting adult female mass as measurements from overhead and side perspectives. This may have been because the spine of adult females was usually curved when they are in a relaxed position, as seen in Fig. 2a. From the end perspective, slight differences in the curvature of the body could have significant effects on the maximum outline of the body, and thus the measurements taken from those photographs. Reaction by seals to the positioning of the scaling pole tended to worsen this problem. Slight differences in the alignment of the camera could have a similarly large effect on the variability of measurements from this perspective. For these reasons, end perspective photographs were not collected in 2003. However, without immobilization, overhead photographs of the type utilized in this study may not be possible to collect on many pinniped species, and therefore an end perspective photograph would likely be useful, as suggested by Bell et al. (1997) and Haley et al. (1991). Comparatively, models from this study (models 1 – 4, Table 1) did not perform as well as models from previous studies that contained only analogous variables. This is

likely a result of the relatively small sample size of end perspective photographs I collected, and again, because of the difficulty associated with taking end perspective photographs of non-immobilized, relatively active, subjects.

Similar to Haley et al. (1991) and Bell et al. (1997), SA was the single best predictor of adult mass in the category two observations. Prior to beginning research, I hypothesized the OA measurement would be the single best predictor of mass because it could account for length and width at once, as does SA, but it might also pick up the affects of gravity on the blubber of very large seals. In fact, the SA, OW, and OA measurements all performed similarly well in describing the variability in mass from category two and three observation. For the estimation of adult female mass from overhead and side photographs that meet the category 2 criteria, I recommend using model 10 (Table 1). The prediction interval around this model of  $\pm 13.8\%$  of adult female mass compares favorably to the analogous confidence interval reported by Haley et al. (1991) of  $\pm 12\%$  around their best model of adult male northern elephant seal mass. For adult female Weddell seals, the difference between predictive ability of the best models derived from category 2 and category 3 datasets was large. This demonstrates the need to collect photographs from seals only when they exhibit as close to typical body and head positions as possible, and are laying on relatively smooth ice or snow. Gathering only photographs of seals that meet category 1 criteria would either reduce the number of samples successfully collected or greatly increase the amount of time spent with each animal, thereby defeating the purpose of using this method. Models of adult female mass may also have some utility for predicting mass of adult male Weddell seals as there is little difference in the general body shape and size between the two sexes (Riedman

1990). This would necessarily assume that the body composition of adult male and female Weddell seals is relatively similar, which has not been evaluated.

Models of pup mass derived from only overhead perspective measurements performed better than models derived from both overhead and side perspective measurements. I suspect this is because models derived from only overhead perspective measurements included more observations at lighter mass, where variability was less. The single best predictor for all categories of pup observations was OW. It only slightly outperformed OA, which again, I had expected to be the best single predictor of pup mass. For the estimation of pup Weddell seal mass from overhead photographs that meet the category 2 criteria, I recommend using model 16 (Table 2). This model had the narrowest prediction intervals of all models of pup mass including those with variables from both overhead and side perspectives. Additionally, utilization of a model that requires measurements from only one photographic perspective is desirable because it would cut in half the photo acquisition and processing time for sampling pups.

For Weddell seals, the photographic method developed here requires less disturbance to individuals than the estimation of mass through direct morphometric measurements or the collection of actual mass measurements. The method does not require chemical immobilization or restraint, and it can be applied to portions of the population most interesting to demographic studies, namely mothers and their pups. The techniques developed here are efficient enough to be applied on a population-wide scale over a short period of time, while the duration of visitations to colonies can be significantly reduced compared to gathering masses using traditional methods. These models should be useful on virtually all individuals within the population because the

range of mass measurements included in the models encompass nearly the entire range of masses recorded for this species (Castellini and Kooyman 1990, Braun-Hill 1987, Tedman and Green 1987, Tedman and Bryden 1979). However, the number of observations of adult females over 550 kg used to derive model 10 (Table 1) was limited, and if more mothers of this size are encountered, collection of a physical mass measurement along with photographs from the overhead and side perspectives would allow refinement of the model.

Because some seals reacted strongly to the positioning of the scaling pole next to them, eliminating the use of a scaling pole could greatly improve the image acquisition process. One alternative may be to project two or more laser dots aligned parallel to each other, at a fixed distance apart, onto the seal during photography. Images could also be scaled using a technique involving calculations based on distance to subject and focal length measurements collected with each photograph. However, this alternative could be more difficult to manage in the field and would increase the processing time of images. One other improvement that could significantly reduce the image analysis time would be the use of infrared cameras. Using these cameras, the contrast between seals and their background could greatly increased allowing further automation of the image analysis process. The emissive properties of seals may differ by species and ambient temperature, so testing would need to be performed before infrared cameras were selected for extensive use. Difficulties associated with scaling photos taken using an infrared camera would also need to be overcome. With or without minor equipment alterations and further refinement of the adult model with additional 550+ kg animals, the methods developed here can now be applied in consideration of interesting biological questions.

For instance, it has been demonstrated that heavier pups at weaning have an energetic advantage over lighter pups and show increased survival to two years of age in some pinnipeds (Baker and Fowler 1992, Craig and Ragen 1999, Muelbert et al. 2003). Therefore, Weddell seal cohorts may experience reduced survival in years where mean maternal parturition mass or post-weaning pup mass is below average. Although the post-weaning mass of pups may be a better indicator of their survival probability, it can be difficult to locate and photograph pups on smooth, safe ice that late in the Antarctic summer. There is also some debate as to the amount or nature of feeding by maternal females during the nursing period. Data presented by Braun-Hill (1988) and Testa et al (1989) concerning mass transfer efficiencies suggests some females must have fed during the nursing period in order to accomplish the high observed efficiency for that pair. The sample of ten dyads photographed through the duration of the nursing period provides a limited example of how this technique may be applied in consideration of these types of questions, and the limitations of data collected in this manner.

The mean rate of mass lost by adult females ( $4.0 \text{ kg d}^{-1}$ ) and gained by pups ( $1.5 \text{ kg d}^{-1}$ ) (Table 3), from the ten dyads photographed throughout the nursing period was less than, but similar to, the  $4.5 \text{ kg d}^{-1}$  and  $4.7 \text{ kg d}^{-1}$  lost by adults and  $2.0 \text{ kg d}^{-1}$  and  $1.9 \text{ kg d}^{-1}$  gained by pups reported by Braun-Hill (1987), and Tedman and Green (1987) respectively. When only the data from the seven experienced mothers and their pups was considered, the result of  $4.5 \text{ kg lost d}^{-1}$ , and  $1.7 \text{ kg gained d}^{-1}$ , respectively, compared more favorably to previous studies. The three lightest females at parturition produced significantly lighter pups at weaning, and the relationship between adult female parturition mass and pup weaning mass was positive and strong ( $r^2 = 0.72$ ,  $F = 20.64$ ,  $P =$

0.002). Confounding this is the fact that the three lightest females at parturition were also the three youngest females. These three adults were producing their first known pup and improved breeding performance with age has been documented in northern elephant seals (Sydeman and Nur 1994, Reiter et al. 1981) and numerous other species (Clutton-Brock 1984). Age and weight at parturition likely covary in the first few years a female is reproductively active because she may not be fully physically matured (Bryden et al. 1984, Guinness et al. 1978). The significantly lighter weaning mass of some pups in the population, or mean weaning mass of entire cohorts, may therefore result from either their mother's mass at parturition, her maternal experience, or both.

Prior to discussion of mass transfer efficiency values, it should be noted that the duration of the weaning period observed among the ten pairs varied significantly (24-40 days). If I had used arbitrary cutoff dates for weaning similar to those used by Braun-Hill (1987) and Testa et al. (1989), I would have obtained very different results. Prior to the collection of mass information for efficiency calculations using predetermined cutoff dates for weaning, investigators should therefore consider the amount of variability in nursing period within their population. If cutoff dates are used, they should be short enough to ensure that no pups have yet been weaned when final weaning masses are collected.

The mean value of mass transfer efficiency for this study (38%) was lower than, but near to, the 43.5% and 47.5% reported by Tedman and Green (1987) and Testa et al. (1989) and was not significantly different between experienced and inexperienced dyads. The similarity of mass transfer values, in this relatively small study compared to those of previous studies with larger sample sizes, (Braun-Hill 1987, Tedman and Green 1987,

Testa et al. 1989) suggests that although prediction intervals around individual mass estimates are wide, the point estimates are quite reliable. Additionally, the ability to collect large samples of mass estimates through the use of this method may compensate for the uncertainty around individual point estimates as shown by the significant differences in mean values between even small samples of experienced and inexperienced dyads (Table 3). However, because mass transfer efficiency calculations involve a ratio of estimated values, overall variance around individual efficiency estimates is inflated. Therefore, this method of mass estimation cannot provide an accurate or precise enough efficiency estimate to compare among individuals. Mean transfer efficiency values from different portions of the population, however, could be tested, as I demonstrated in the experienced versus inexperienced comparison (Table 3). Annual variation in population wide means, such as maternal parturition mass or post-weaning pup mass, can be detected using the photographic method, as demonstrated by the power analysis.

Values concerning mass transfer in this study were consistently lower than those reported in previous studies on Weddell seals. This may be a result of having sampled in a year in which adult females arrived at the pupping colonies lighter than usual. This is supported by the significantly lighter mean maternal parturition mass in 2003 as compared to 2002 ( $\bar{x}_{2002} = 456 \text{ kg}$  ( $n = 15$ ),  $\bar{x}_{2003} = 405 \text{ kg}$  ( $n = 33$ ),  $t = 2.42$ ,  $P = 0.026$ ), and a mean age that did not differ significantly between those years ( $\bar{x}_{2002} = 13.3 \text{ yrs}$  ( $n = 10$ ),  $\bar{x}_{2003} = 10.7 \text{ yrs}$  ( $n = 13$ ),  $t = 1.61$ ,  $P = 0.122$ ). If pup weaning mass is both a function of the mother's parturition mass and a predictor of pup survival, then such

annual variation in mean maternal parturition mass may be a useful indicator of pup cohort survival.

Weddell seal population vital rates could be directly linked to environmental variability through effects on food resources if the body mass of seals is found to change in relation to environmental fluctuations known to affect those food resources. Large scale fluctuation in the southern ocean has been correlated with changes in the concentrations and availability of Antarctic krill and other basal food resources (Loeb et al. 1997, Siegel and Loeb 1995, Pakhomov and McQuaid 1996). Relationships between environmental parameters, especially sea-ice extent, and population vital rates, have also been demonstrated for numerous sea bird and seal populations (Croxall et al. 2002, Testa et al. 1991, Weimerskirch et al. 2003). This suggests a link between environmental fluctuation and predator populations through food availability. Because Weddell seal food availability in McMurdo Sound is difficult to measure directly, the acquisition of annual maternal parturition mass estimates over a long period of time may provide a surrogate measure or index of regional availability of food resources. If environmental fluctuations that affect food resources are found to correlate with female parturition mass or post-weaning pup mass and subsequent cohort survival, then pathways directly affecting the Weddell seal population dynamics of Erebus Bay may be detected with implications for other marine predators.

LITERATURE CITED

- Anderson, S. S., and M. A. Fedak. 1987. Grey seal, *Halichoerus grypus*, energetic: females invest more in male offspring. *Journal of Zoology* **211**:667-679.
- Baker, J. D., and C. W. Fowler. 1992. Pup weight and survival of northern fur seals *Callorhinus ursinus*. *Journal of Zoology* **227**:231-238.
- Bell, C. M., M. A. Hindell, and H. R. Burton. 1997. Estimation of body mass in the southern elephant seal, *Mirounga leonina*, by photogrammetry and morphometrics. *Marine Mammal Science* **13**:669-682.
- Bowen, W. D., D. J. Boness, and O. T. Oftedal. 1987. Mass transfer from mother to pup and subsequent mass loss by the weaned pup in the hooded seal, *Cystophora cristata*. *Canadian Journal of Zoology* **65**:1-8.
- Braun-Hill, S. E. 1987. Reproductive ecology of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. Ph. D. University of Minnesota, Minneapolis.
- Brierley, A. S., P. G. Fernandes, M. A. Brandon, F. Armstrong, N. W. Millard, S. D. McPhail, P. Stevenson, M. Pebody, J. Perrett, M. Squires, D. G. Bone, and G. Griffiths. 2002. Antarctic krill under sea ice: elevated abundance in a narrow band just south of the ice edge. *Science* **295**:1890-1892.
- Bryden, M. M., M. S. R. Smith, R. A. Tedman, and D. W. Featherston. 1984. Growth of the Weddell seal, *Leptonychotes weddelli* (Pinnipedia). *Australian Journal of Zoology* **32**:33-41.
- Cameron, M. F. 2001. Dynamics of a Weddell seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. Ph. D. University of Minnesota, Minneapolis.
- Casella, G., and B. L. Berger. 2002. *Statistical Inference*, Second edition. Duxbury, Pacific Grove.
- Castellini, M. A., R. W. Davis, and G. L. Kooyman. 1988. Blood-chemistry regulation during repetitive diving in weddell seals. *Physiological Zoology* **61**:379-386.

- Castellini, M. A., and G. L. Kooyman. 1990. Length, girth and mass relationships in Weddell seals (*Leptonychotes weddellii*). *Marine Mammal Science* **6**:75-77.
- Clutton-Brock, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. *American Naturalist* **123**:212-229.
- Craig, M. P., and T. J. Ragen. 1999. Body size, survival, and decline of juvenile Hawaiian monk seals, *Monachus schauinslandi*. *Marine Mammal Science* **15**:786-809.
- Crocker, D. E., J. D. Williams, D. P. Costa, and B. J. LeBoeuf. 2001. Maternal traits and reproductive effort in northern elephant seals. *Ecology* **82**:3541-3555.
- Croxall, J. P., P. N. Trathan, and E. J. Murphy. 2002. Environmental change and antarctic seabird populations. *Science* **297**:1510-1514.
- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* **31**:367-393.
- Guinness, F. E., T. H. Clutton-Brock, and S. D. Albon. 1978. Factors affecting calf mortality in red deer (*Cervus elaphus*). *Journal of Animal Ecology* **47**:817-832.
- Guinet, C., P. Jouventin, and J. Y. Georges. 1994. Long term population changes of fur seals *Arctocephalus gazella* and *Arctocephalus tropicalis* on subantarctic (Crozet) and subtropical (St Paul and Amsterdam) islands and their possible relationship to El Nino Southern Oscillation. *Antarctic Science* **6**:473-478.
- Haley, M. P., C. J. Deutsch, and B. J. Le Boeuf. 1991. A method for estimating mass of large pinnipeds. *Marine Mammal Science* **7**:157-164.
- Hunt, B. P. V., E. A. Pakhomov, and C. D. McQuaid. 2001. Short-term variation and long term changes in the oceanographic environment and zooplankton community in the vicinity of a sub-Antarctic archipelago. *Marine Biology* **138**:369-381.

- Iverson, S. J., W. D. Bowen, D. J. Boness, and O. T. Oftedal. 1993. The effect of maternal size and milk energy output on pup growth in grey seals (*Halichoerus grypus*). *Physiological Zoology* **66**:61-68.
- Jenouvrier, S., C. Barbraud, and H. Weimerskirch. 2003. Effects of climate variability on the temporal population dynamics of southern fulmars. *Journal of Animal Ecology* **72**:576-587.
- Kooyman, G. L. 1981. Weddell seal - consummate diver. Cambridge University Press, Cambridge, England.
- Kovacs, K. M., and D. M. Lavigne. 1992. Mass-transfer efficiency between hooded seal (*Cystophora cristata*) mothers and their pups in the Gulf of St. Lawrence. *Canadian Journal of Zoology* **70**:1315-1320.
- Laws, R. M., editor. 1993. Antarctic Seals: research methods and techniques. Cambridge University Press, Cambridge.
- Le Boeuf, B. J., R. Condit, and J. Reiter. 1989. Parental investment and the secondary sex ratio in northern elephant seals. *Behavioral Ecology and Sociobiology* **25**:109-117.
- Loeb, V. J., V. Siegel, O. Holm-Hansen, R. Hewitt, W. Fraser, W. Trivelpiece, and S. Trivelpiece. 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* **387**:897-900.
- Mellish, J.-A. E., S. J. Iverson, and W. D. Bowen. 1999. Variation in milk production in lactation performance in grey seals and consequences for pup growth and weaning characteristics. *Physiological and Biochemical Zoology* **72**:667-690.
- Modig, A. 1995. Social behaviour and reproductive success in southern elephant seal (*Mirounga leonina*). Ph.D. Stockholm University, Stockholm.
- Muelbert, M. M. C., W. D. Bowen, and S. J. Iverson. 2003. Weaning mass affects changes in body composition and food intake in harbour seal pups during the first month of independence. *Physiological and Biochemical Zoology* **76**:418-427.

- Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models, Fourth Edition edition. McGraw-Hill, Boston, Massachusetts.
- Pakhomov, E. A., and C. D. McQuaid. 1996. Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biology* **16**:271-286.
- Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge.
- Ponganis, P. J., G. L. Kooyman, M. A. Castellini, E. P. Ponganis, and K. V. Ponganis. 1993. Muscle temperature and swim velocity profiles during diving in a Weddel seal, *Leptonychotes weddellii*. *Journal of Experimental Biology* **183**:341-346.
- Priddle, J., J. P. Croxall, I. Everson, R. B. Heywood, E. J. Murphy, P. A. Prince, and C. B. Sear. 1988. Large-scale fluctuations in distributions and abundance of krill -- a discussion of possible causes. Pages 169-182 in D. Sahrhage, editor. Antarctic Ocean and resource variability. Springer-verlag, Berlin.
- Reiter, J., N. L. Stinson, and B. L. Boeuf. 1981. Female competition and reproductive success in northern elephant seals. *Behavioural Ecology and Sociobiology* **3**:337-367.
- Riedman, M. 1990. The pinnipeds: seals, sea lions, and walruses. University of California Press, Berkely California.
- Sæther, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology and Evolution* **12**:143-149.
- Scheffer, V. B. 1967. Standard measurements of seals. *Journal of Mammalogy* **48**:459-462.
- Siegel, V., and V. Loeb. 1995. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Marine Ecology Progress Series* **123**:45-56.

- Stirling, I. 1969. Ecology of the Weddell seal in McMurdo Sound, Antarctica. *Ecology* **50**:573-586.
- Sydeman, W. J., and N. Nur. 1994. Life History strategies of female northern elephant seals. Pages 137-153 *in* R. M. Laws, editor. *Elephant seals: population ecology, behavior, and physiology*. University of California Press, Berkeley, California, USA.
- Team, R Development Core. 2004. R: A language and environment for statistical computing, version 1.9.1. R Foundation for Statistical Computing, Vienna, Austria.
- Tedman, R. A., and M. M. Bryden. 1979. Cow-pup behaviour of the Weddell seal, *Leptonychotes weddelli*, in McMurdo Sound, Antarctica. *Australian Wildlife Research* **6**:19-37.
- Tedman, R. A., and B. Green. 1987. Water and sodium fluxes and lactational energetics in suckling pups of Weddell seals (*Leptonychotes weddellii*). *Journal of Zoology* **212**:29-42.
- Testa, J. W. 1986. Long term patterns in life history characteristics and population dynamics of weddell seal (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. Ph.D. University of Minnesota, Minneapolis.
- Testa, J. W., E. B. Hill, and D. B. Siniff. 1989. Diving behavior and maternal investment in Weddell seals (*Leptonychotes Weddellii*). *Marine Mammal Science* **5**:399-405.
- Testa, J. W., G. Oehlert, D. G. Ainley, J. L. Bengtson, D. B. Siniff, R. M. Laws, and D. Rounsevell. 1991. Temporal variability in Antarctic marine ecosystems: periodic fluctuation in the phocid seals. *Canadian Journal of Fisheries and Aquatic Sciences* **48**:631-639.
- Testa, J. W., and D. B. Siniff. 1987. Population Dynamics of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. *Ecological Monographs* **57**:149-165.

Thompson, P. M., and J. C. Ollason. 2001. Lagged effects of ocean climate change on fulmar population dynamics. *Nature* **413**:417-420.

Weimerskirch, H., I. P. C. Guinet, and B. C. 2003. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Science* **15**:249-256.

APPENDICES

APPENDIX A

Intra- and Inter- Coefficients of Variation from each Photographic Perspective

Table 1. Average intra-image coefficient of variation of each measurement from each perspective after repeating the image calibration and measurement process five times each on 10 randomly selected images from each perspective.

<b>Average Coefficient of Variation (in %)</b>				
<b>Measurement</b>	<b>Perspective</b>			<b>Average</b>
	<b>OH</b>	<b>Side</b>	<b>End</b>	
Area	0.19	0.41	0.46	0.35
Length	0.27	0.43	-	0.35
Width/Height	0.45	0.66	0.21	0.44
Girth	-	-	0.49	0.49
Average	0.30	0.50	0.38	0.40

Table 2. Average inter-image coefficient of variation from multiple images of the same seal taken immediately after each other, in which the seal had not changed head or body position. Ten suites of images were used from each perspective.

<b>Average Coefficient of Variation (in %)</b>				
<b>Measurement</b>	<b>Perspective</b>			<b>Average</b>
	<b>OH</b>	<b>Side</b>	<b>End</b>	
Area	1.46	1.11	2.70	1.76
Length	0.89	0.83	-	0.86
Width/Height	0.91	1.26	1.25	1.14
Girth	-	-	1.33	1.33
Average	1.09	1.07	1.76	1.30

APPENDIX B

Estimates of Mass from 10 Dyads Photographed Throughout the Nursing Period

Figure 1. Maternal female mass and (A), and pup mass (B) for ten mother pup pairs photographed every five days during the nursing period. Initial weights were physical measurements while all other weights were estimated using model 10 (Table 1) for adults, and model 16 (Table 2) for pups. Pups are listed in the legend in corresponding order to their associated mother. Dashed lines indicate the three dyads for which this was the mother's first known pup.

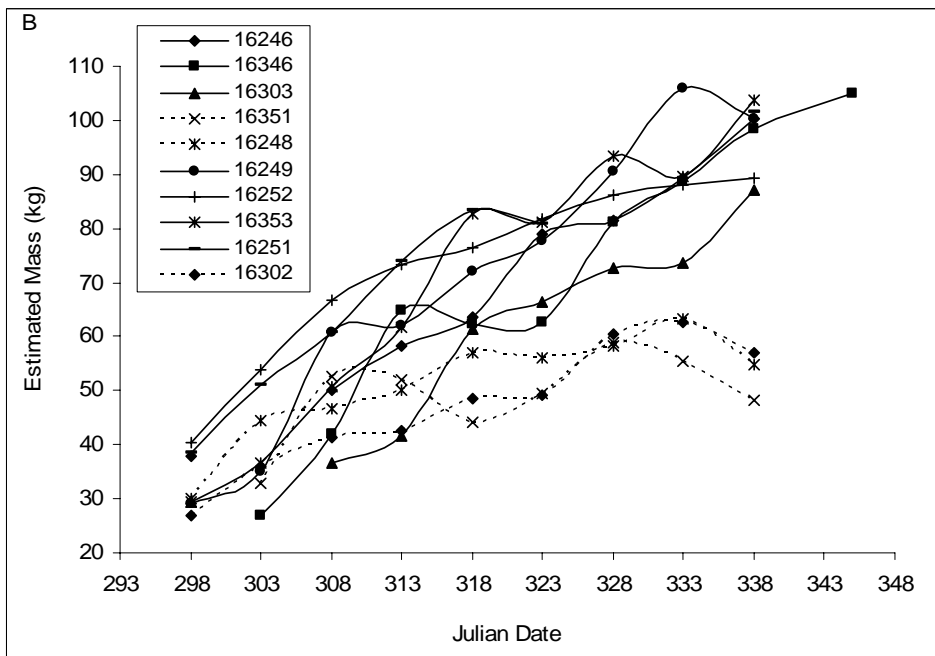
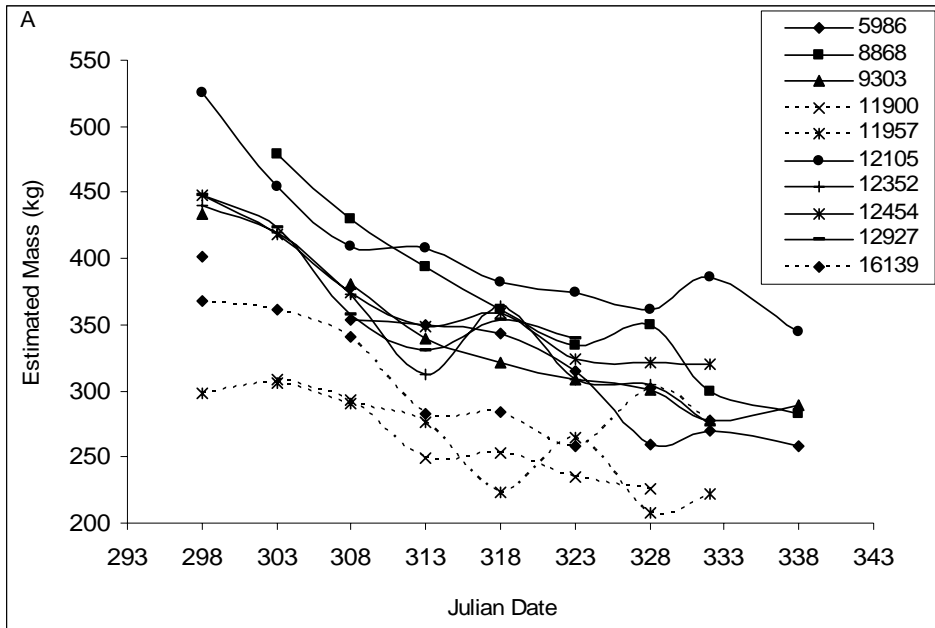




Table 2. Parturition and weaning mass of individuals from ten dyads photographed throughout the 2003 nursing period. Parturition mass was a true physical measurement while all other weights were estimated from photographic measurements using model 10 (Table 1) for adults and model 16 (Table 2) for pups. Prediction intervals are given in kilograms and apply to both the weaning mass and the mass gained/lost values. Experienced dyads ( $\text{mean}_{\text{exp}}$ ) were those in which the adult female has had at least two previous pups. Inexperienced dyads ( $\text{mean}_{\text{inexp}}$ ) are those in which this is the first known pup for that adult female (Maternal Seal ID 11900, 11957, and 16139). Pups are listed directly below their associated mother. Differences between means were tested using Scheffe's procedure with a family  $\alpha$  of 0.05.

	Maternal Seal ID										overall mean (n=10)	$\text{mean}_{\text{exp}}$ (n=7)	$\text{mean}_{\text{inexp}}$ (n=3)	difference
	5986	8868	9303	11900	11957	12105	12352	12454	12927	16139				
age or year tagged	20	14	13	7	7	1996	1997	1997	1997	2002				
# previous known pups	8	7	6	0	0	6	3	4	2	0				
parturition mass	402	479	434	308	298	525	440	448	448	368.5	415.1	453.7	324.8	128.9*
weaning mass	254.8	279.9	285.3	223.1	219.1	340.4	271.4	316.3	334.6	273.4	279.8	297.5	238.5	59.0**
± 95% PI (kg)	50.4	50.1	50.1	50.9	50.8	50.9	50.0	50.5	49.7	51.8	30.3	30.8	44.9	
mass lost	147.2	199.1	148.7	84.9	78.9	184.6	168.6	131.7	113.4	95.1	135.2	156.2	86.3	69.9**
duration of lactation	40	34	40	24	34	40	34	34	25	34	33.9	35.3	30.7	4.6
mass lost per day	3.7	5.9	3.7	3.5	2.3	4.6	5.0	3.9	4.5	2.8	4.0	4.5	2.9	1.6
% loss	36.6	41.6	34.3	27.6	26.5	35.2	38.3	29.4	25.3	25.8	32.0	34.4	26.6	7.8
	Pup Seal ID													
	16246	16346	16303	16351	16248	16249	16252	16353	16251	16302				
parturition mass	38	27	29.5	33	30	29	40.5	29.5	38.5	27	32.2	33.1	30.0	3.1
weaning mass	100.9	99.0	87.6	59.1	63.6	100.7	88.4	90.1	81.2	62.8	83.3	92.6	61.9	30.7**
± 95% PI (kg)	19.4	19.2	18.0	14.7	15.3	19.4	18.1	18.7	17.4	15.2	9.7	6.1	4.2	
mass gained	62.9	72.0	58.1	26.1	33.6	71.7	47.9	60.6	42.7	35.8	51.1	59.4	31.9	27.6**
duration of lactation	40	34	40	24	34	40	34	34	25	34	33.9	35.3	30.7	4.6
mass gained per day	1.6	2.1	1.5	1.1	1.0	1.8	1.4	1.8	1.7	1.1	1.5	1.7	1.0	0.6
% gain	165.5	266.8	196.9	79.1	112.1	247.1	118.2	205.5	111.0	132.7	163.5	187.3	108.0	79.3
transfer efficiency (%)	42.7	36.2	39.1	30.7	42.6	38.8	28.4	46.0	37.7	37.7	38.0	38.4	37.0	1.4
± 95% PI (%)	13.6	8.8	12.1	21.4	37.3	10.2	10.8	17.2	16.2	23.0	3.8	4.5	8.0	

\* $P < 0.05$ , \*\* $P < 0.001$