CHAPTER ONE:
GENERAL INTRODUCTION

Introduction

An adequate study of animal population biology requires an understanding of population dynamics (Lebreton et al. 1993). The major objective in studies of population dynamics is to detect and analyse differences in life history traits among groups of individuals through temporal and spatial scales (Lebreton et al. 1992). Such differences affect rates of population change through changes in survival and fecundity (Siniff et al. 1977). The detection of these changes may indicate large-scale shifts in ecosystem processes (Weimerskirch et al. 2003; McMahon and Burton 2005). Long-term monitoring programmes are ideal to trace the fate of numerous animals within the population from birth throughout life (i.e. longitudinal life history studies) (Clobert et al. 1994).

A great deal of research has in recent years been aimed at demographic aspects of the Marion Island southern elephant seal population as a long-term longitudinal dataset is in existence (1983 – present). The focus has in particular been on changes in population sizes (Bester and Wilkinson 1994; Pistorius et al. 1999a), and causal factors contributing to these changes, both proximate and ultimate (Bester and Wilkinson 1994; Pistorius et al. 1999b). The Marion Island elephant seal population has declined by 83% since 1951 (Laws 1994) and by 37.2% between 1986 and 1994 at an annual rate of change of 5.8%, which was linear over the period (Pistorius et al. 1999a). Pistorius et al. (1999b, 2001, 2008) suggested a change in population trend, from decrease to stability, around 1994. Bradshaw et al. (2002) argued that this conclusion was preliminary, based on a limited timeline of data. Subsequently, McMahon et al. (2005a, 2009) argued that the population trend inflexion point was situated around 1998. Pistorius et al. (1999a, 1999b, 2001a, 2001b, 2002, 2004, 2005, 2008a, 2008b) and Pistorius and Bester (2002a, 2002b) tested several hypotheses to understand what could be driving the regulation of the Marion Island elephant seal population, ultimately concluding that adult female survival due to food limitation was the proximate cause of the decline in the population. McMahon et al. (2003, 2005b) contended that juvenile survival was of greater importance in both the decline and recent stabilization (McMahon et al. 2009) of this population. Notwithstanding the significant contribution that these studies have made to understanding the demographic drivers of southern elephant seal population rates at this locality, their limited temporal data, assumptions of various life-history parameter states, and the contention that has arisen from these studies demand further in-depth exploration of life history parameters for this population.

Southern Elephant Seal Biology

Southern elephant seals (*Mirounga leonina*) belong to the family phocidae (Order: Pinnipedia) and share the genus *Mirounga* with the northern elephant seal (*M. angustirostris*) (Le Boeuf and Laws 1994). These species are extreme capital breeders (Boyd 2000). Southern elephant seals are the largest living pinnipeds (King 1983) and portray strong sexual dimorphism, with adult males (3000 – 4000 kg) weighing up to 10 times more than adult females (400 – 900 kg) (Laws 1953). Breeding and mating is cyclic and females commence with their first mating attempts between the ages of 2 and 6 years while males, although sexually mature at age ~ 4, become socially mature after age 7 (Laws 1953; Condy 1979). The mating system of the species is strongly polygynous, with an often large 'herd/harem' of females congregating on a haul-out beach and guarded and mated by adult bulls at ratios (cows:bulls) varying from 9:1 (Wilkinson and van Aarde 1999) to 277:1 (Carrick et al. 1962), depending on the locality. Males do not contribute to the growth or rearing of offspring. Females give birth to a single pup (weighing as much as 40 – 46 kg) about a week after hauling out (Laws 1993) and wean the pup in 3 weeks during which time a substantial transfer of energy takes place (Fedak et al. 1996). The harem master mates with the cow at approximately the time of weaning of her pup, after which she departs to sea (Condy 1979). It is not known whether first mating in life occurs at sea, given the absence of juvenile cows from the breeding harems. Southern elephant seals undergo two, sometimes three, fasting periods during the course of one year in the breeding, moulting and winter haulouts (Condy 1979; Kirkman et al. 2001, 2003, 2004).

Southern Elephant Seal Distribution

Southern elephant seals are distributed in the Southern Ocean region between about 35°S and 70°S (Laws 1994) (Fig. 1.1). They haul-out onto sub-Antarctic islands and some mainland sites on the coasts of Argentina and Antarctic to breed, moult and over-winter (Laws 1994; McMahon et al. 2005a).

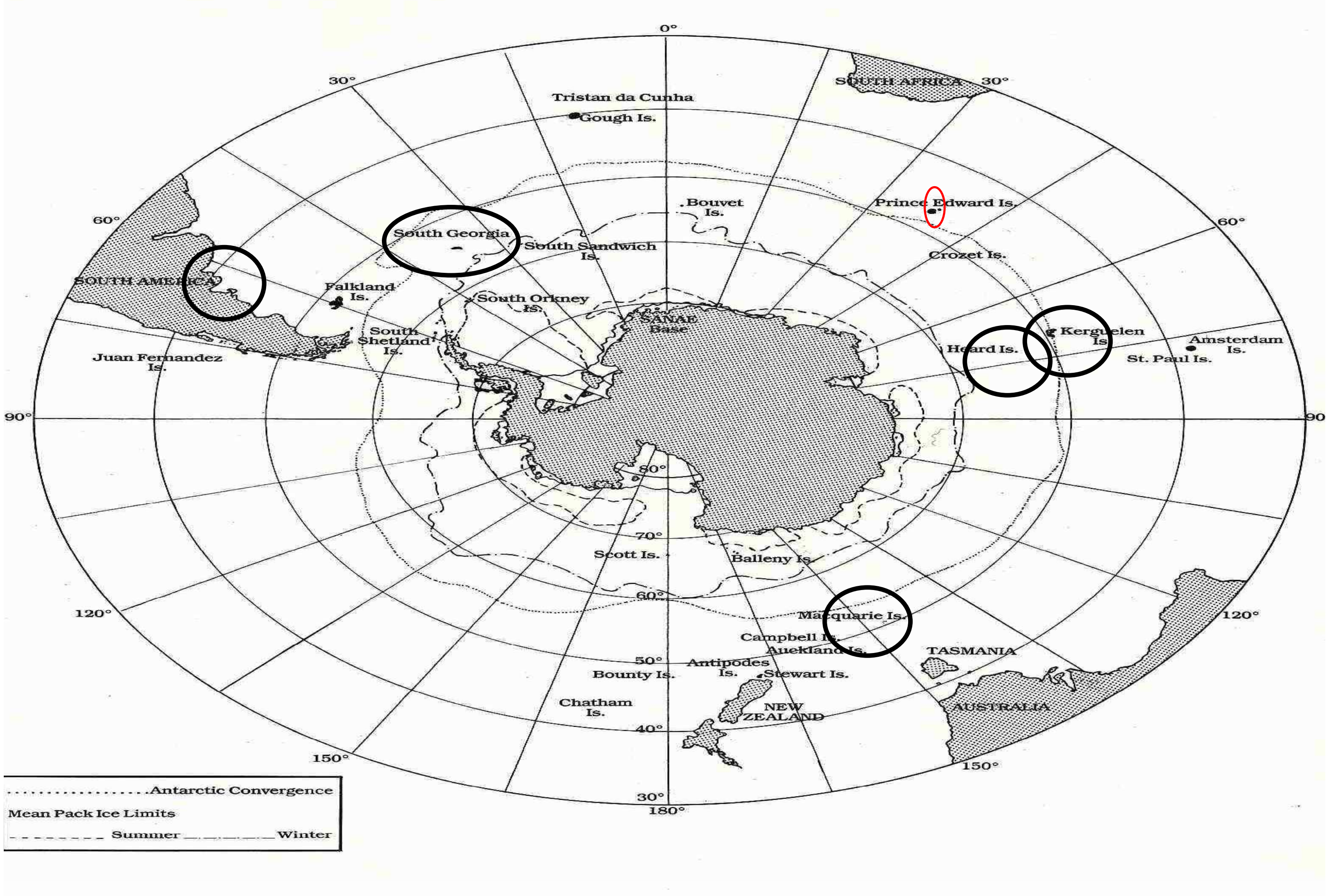

Fig. 1.1. Distribution of the five largest populations of southern elephant seals (large circles indicating relative population sizes). The smallest circle (red) illustrates the position of the small Prince Edward Islands population. Antarctica is displayed in the centre of the map.

The global population of southern elephant seals is divided into four genetically distinct sub-populations or “stocks”, namely the 1) Peninsula Valdés - Argentina, 2) South Georgia, 3) Kerguelen, and 4) Macquarie stocks (Slade et al. 1998; Hoelzel et al. 2001) (Fig. 1.1). The elephant seals on Marion Island form part of the Kerguelen or South Indian Ocean stock.

Present Worldwide Population Status

Ninety-eight percent of the global stock of southern elephant seals, are comprised of the South Georgia population, the Heard and Kerguelen islands populations, Macquarie Island and Peninsula Valdés populations (McMahon et al. 2005a). The remaining 2% of the global population consist of small subpopulations occurring on islands throughout the Subantarctic and adjoining regions (Laws 1994), including the population of interest in this study at Marion Island.

The South Georgia population (the largest globally) has remained stable since 1951. The Kerguelen stock, comprised of six island subpopulations has experienced precipitous declines since the 1950s, although recent evidence suggests most of these populations have stabilized during the 1990s. The Macquarie Island stock has experienced a similarly steep decline, while the only mainland centred population, at Peninsula Valdés is also the only population that has increased for the past few decades (reviewed in McMahon et al. 2005a). The most recent two reviews of the global population status in this species, documented these mainly declining trends pre-1990’s (Laws 1994; McMahon et al. 2005a), while the period between these reviews (1994 - 2003) seems to have seen a stabilisation in the global population at around 740 000 southern elephant seals (McMahon et al. 2005a).

Study Area and Marine Surrounds

Subantarctic Marion – and smaller Prince Edward Island, encompasses the Prince Edward Islands (PEIs) archipelago. The islands are situated approximately 22km apart, with Marion Island (46^{o}54’S, 37^{o}45’E) located southeast of its sister island. The islands are emerged, quasi-active volcanic islands in the Southern Ocean, about half way between South Africa and the Antarctic Continent (Fig. 1.1). The islands are governed under the sovereignty of South Africa.

The PEIs are situated within the Polar Frontal Zone (PFZ), in the direct path of the Antarctic Circumpolar Current (ACC), bounded to the north and south by the dynamically changing Subantarctic Front (SAF) and Antarctic Polar Front (APF) respectively (Lutjeharms and Valentine 1984). The islands are situated along the south-west Indian ridge, a series of undersea mountain ranges and fracture zones or canyons that stretches from the mid-Atlantic ridge in the west to the central Indian ridge in the east. These bathymetrical features interact with the ACC to form eddies, which enhance the mesoscale variability in this region of the Southern Ocean (Lutjeharms and Valentine 1988). Pockets of cold water (cyclonic eddies) from south of the APF and warmer waters (anticyclonic eddies) from north of the SAF are responsible for carrying foreign organisms into the ACC (Froneman et al. 1999, Bernard et al. 2007) and for enhancing the primary productivity of the region.

Marion Island is approximately 300km^2 in area rising to 1240m above sea level (Meiklejohn and Smith 2008), and has a coastline of approximately 90km (Fig. 1.2). The coastline is comprised mostly of volcanic cliff-faces, interspersed with small pebble, boulder or rock-strewn beaches and only two that can be considered sandy, namely Ship's Cove and Goodhope Bay beaches (black beaches). The western half of the island is characterised by mostly vertical cliffs rising directly out of the sea and few rugged beaches, while the eastern half of the island has a gentler transition from sea to land and more accessible beaches. Southern elephant seals occur mainly on the leeward east and north coasts due to the greater availability of haul-out beaches and terraces, although a few sites on the south coast are frequently used (Fig. 1.2) (Condy 1978).

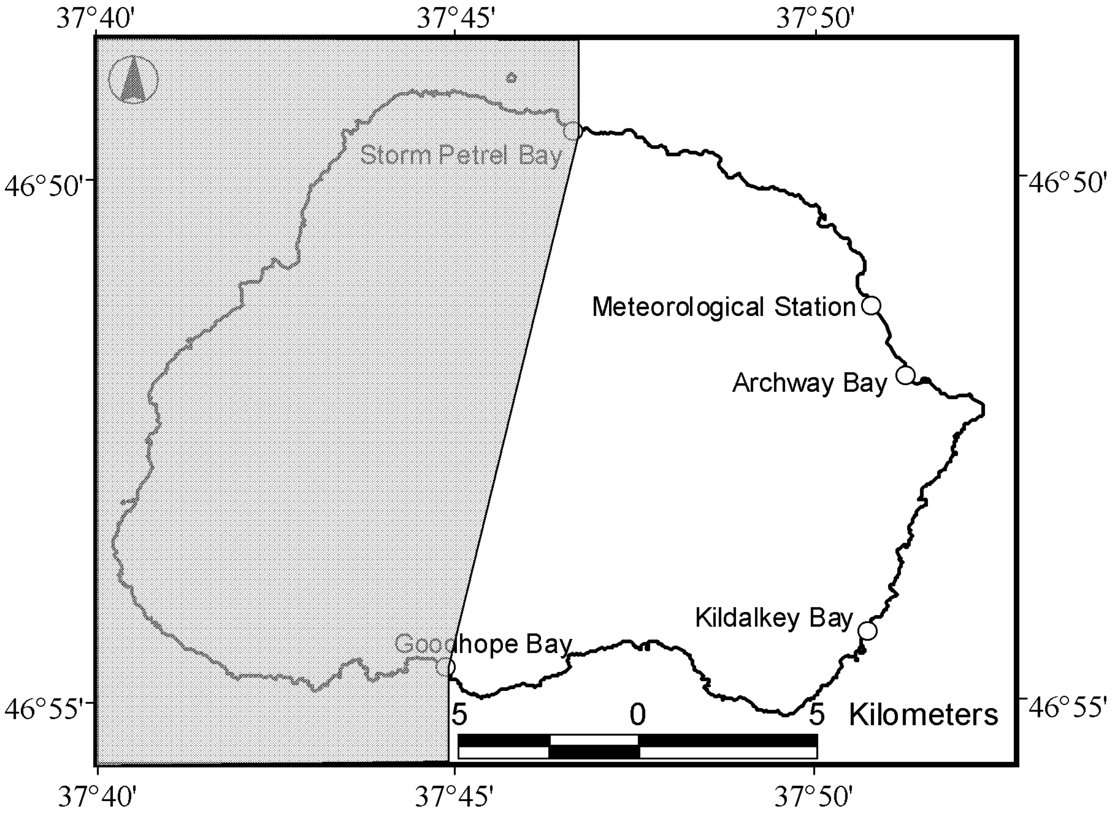

Fig. 1.2. Subantarctic Marion Island (46°54'S, 37°45'E). The unshaded part of the map depicts the coastlines preferred by southern elephant seals for haul-out activities. The unshaded stretch of coastline is traversed regularly on foot for resighting of tagged southern elephant seals. The rugged coastline in the shaded area offers virtually no preferred haul-out beaches to this species.

Large beds of bull kelp, *Durvillaea antarctica*, form an almost continuous ring around the island close inshore (<100m offshore) while further offshore (500 to 1000m offshore) a similar ring of giant kelp, *Macrocystis pyrifera*, surrounds the island. From an elephant seal point of view, these kelp communities are important for two principal reasons. Firstly, they are an important contributor to “wrack beds” composed of storm dislodged kelp fronds that contribute to the temporal accessibility and suitability of certain beaches used by seals. Secondly, these ‘kelp forests’ provide ambushing habitat for killer whales, *Orcinus orca*, (PJNdB personal observation). Killer whales are an important seal predator here (see Appendix 3 - Tosh et al. 2008) close inshore (Fig. 1.3.).

Fig. 1.3. The large kelp beds immediately offshore of Marion Island (left) are depicted. Killer whales, *Orcinus orca*, (foreground) are important predators of southern elephant seals and use these kelp beds for concealment. Prince Edward Island is visible in the top right.

Aims and Objectives of this study

Studies of animal demography are fundamentally anchored in the monitoring and analyses of life history traits of individuals (Lebreton et al. 1992). Yet, such analyses require large numbers of identifiable individuals to be monitored through time, typically in a capture-mark-recapture framework. Large wild mammals are inherently difficult study subjects for individual life history monitoring, because they are often dangerous and difficult to locate, approach or physically handle. The ubiquitous terrestrial phases displayed by pinnipeds (i.e. seals) make them some of the more easily approachable mammalian groups, some species more than others. Southern elephant seals, particularly adult females, show a high degree of site fidelity to their natal island (Bester 1989) making the species ideal for long-term monitoring studies (Bester 1988; Erickson et al. 1993).

During perusal of the population demographic literature at the commencement of this PhD, some methodological limitations were striking. In particular, analyses of life history parameters with body condition (directly related to body mass in southern elephant seals) as covariate, are rare and usually the samples are small. Additionally, methods of identifying relatedness in southern elephant seal populations, in particular the temporal and spatial variation in condition of mothers and their offspring, suffered from small sample sizes. Such limitations impede progress in holistic demographic research. These impediments may be generally restrictive to life history and demography studies, or they could be species - or site specific. The long-term nature of mark-recapture population demographic studies unfortunately results in extended lag times for novel methodological advancements to become useful. Consequently, I use a long-term and valuable mark-recapture dataset for life-history analyses without the latest methodological field improvements presented here. However, these advancements are intentionally presented prior to the population demographic analyses so as to allow the reader the opportunity to relate the potential of these advances to future demographic analyses.

Consequently, the general purpose of this thesis is twofold:

(1) To investigate and advance certain field research techniques of direct relevance to studies of population demography in southern elephant seals and potentially for other large vertebrates.

(2) To investigate/identify life history parameters that are most important for population regulation in the Marion Island population of southern elephant seals, and attempt to clarify existing disputes in this regard.

The specific objectives of this research are to:

1.1) Ease the measurement of body mass for large southern elephant seals, specifically to simplify effort to gain large sample sizes and to allow for broad applicability to various field scenarios. I therefore aim to advance the use of photogrammetry for estimating the individual mass of southern elephant seals.

1.2) Given an inability to assess the relationship in survival and reproductive parameters between mothers and offspring with the current elephant seal dataset, I aim to investigate field methods that would allow the future identification of large samples of pups with known mothers.

1.3) I aim to use the current 25-year longitudinal dataset to determine age- and sex-dependent survivorship in the Marion Island population of southern elephant seals. For comparative purposes I aim to repeat the analytical procedure presented in the earlier survivorship analyses (Pistorius et al. 1999b) that was based on approximately half of the current dataset. That study provided a catalyst for numerous subsequent published works, some of which incite contention about the fundamental demographic drivers of this population. I aim to clarify some of this contention.

1.4) I aim to conduct a study of senescence in these long lived capital breeders, with added emphasis on longevity and fertility in female southern elephant seals at this locality. I aim to address these topics from primarily a population regulation point of view, but also to include life history descriptors that are useful for the evolutionary study of senescence.

1.5) I aim to provide a philosophically angled discussion of the use of sophisticated analytical tools in population demographic studies (specifically mark-recapture). I aim to use an example from the elephant seal dataset to illustrate my argument.

1.6) Finally, I aim to gain a more holistic perspective of the drivers and descriptors of southern elephant seal population dynamics at Marion Island, through initiation of related fields of study. I aim to initiate work on alternative methods of chemical immobilisation of these seals, to further investigation into tag-loss rates in this population of seals, and lastly to gain a better understanding of the population characteristics of the understudied killer whales (as predators of seals) around Marion Island. *(Appendices)*

Several key questions arise as a consequence of these aims and objectives:

a) Can photogrammetry be broadly applicable to mass estimation of seals in many field scenarios and with seals resting in any position, contrary to the *status quo* for the method?

b) What method of photographing seals for ultimate mass estimation can be conducted with minimal manpower and equipment, and is cost-effective?

c) Is it possible to mark large samples of unweaned southern elephant seal pups within congested harems over time, when these harems consist of aggressive mothers and harem-masters?

d) What method of marking unweaned pups can be conducted with minimal manpower and equipment, and be cost-effective and relatively safe for the fieldworker?

e) Has the Marion Island southern elephant seal population stabilised since 1994?

f) What is the survivorship of the population in relation to age, sex and cohort?

g) Is juvenile or adult female survival at Marion Island the major contributing factor in population regulation?

h) Do southern elephant seal females show actuarial senescence, and if so what are the demographic consequences thereof?

i) Is there evidence for reproductive senescence in southern elephant seal females, and if so what are the demographic consequences thereof?

j) What are the observed and predicted longevity and fertility schedules of southern elephant seal females for the Marion Island population?

k) What mark-recapture analyses can (cannot) be performed with program MARK, and what does this mean for science in general?

l) Can ketamine-hydrochloride be used in combination with reversible drugs (other than xylazine) for the immobilisation of elephant seals? *(Appendices)*

m) Does tag-site (on the flipper) affect the rates of tag-loss in southern elephant seals? *(Appendices)*

n) What are the rates of age- and sex-dependent tag-loss for each cohort in this population? *(Appendices)*

o) Is the social organisation of killer whales at Marion Island comparable to the mammal-eating transient sociality of northern hemisphere killer whales? *(Appendices)*

p) What are the consequences of killer whale sociality, for the killer whale prey animals? *(Appendices)*

Thesis Structure

The structure of this thesis follows a progression of firstly, field method advancement for population demographic studies, followed by an investigation of life-history parameters that may be regulating this population, and finally an initiation of studies into broader ecological questions of relevance in population demographic studies.

In Chapter Two, I approach the question of the field estimation of body condition (specifically mass) because it is a fundamental parameter that is valuable for covariate analyses in life-history studies. However, for large southern elephant seals, the estimation of body mass is (at best) possible only with extensive manpower and effort for a small sample of individuals under specific field conditions, or (at worst) impossible if field conditions do not permit access to weigh individuals or if individuals are too large. Photogrammetry has previously been attempted with some success, but limitations persist. I use a large sample of weighed individuals to test a novel three-dimensional photogrammetric body mass estimation approach specifically with broad field applicability in mind.

In Chapter Three, I embark upon a quest to find the simplest, most cost-effective method to individually identify unweaned southern elephant pups. Southern elephant seal pups are simple to mark (with long-term/permanent marks) once they have weaned because they move out of the harem where aggressive adults would impede such marking. However, at that stage the maternal bond has been severed and pups cannot be assigned to respective mothers. A temporary marking technique whereby unweaned pups can be assigned to their known (marked) mothers, to be identifiable upon weaning, is required. Different markers and techniques are evaluated to surmount these field limitations.

Chapters Two and Three, thereby address two major obstacles in population demographic research on southern elephant seals at Marion Island, and should, over time increase the robustness of the mark-recapture work to gain a better understanding of population regulation.

Chapter Four, uses the existing 25-year longitudinal mark-recapture (resight) dataset for this species at Marion Island, to advance on the 15-year survivorship results presented for this same population by Pistorius et al (1999b). A modelling approach using program MARK is employed to gain insight into life-history parameter estimates. The fortuitous temporal setting of the current dataset, encompassing both periods of decline and increase in the population, provides a solid foundation for additional investigation of the contention surrounding the drivers of the population. I therefore attempt to clarify the role that juveniles and adult females play in regulation of this population.

In Chapter Five, I investigate whether female southern elephant seals portray either actuarial or reproductive senescence. I also add relevant investigations and descriptions of longevity and fertility of female seals from this population. The significance of these life-history traits are discussed in relation to their importance for, and possible regulating role in population demography.

Chapters Four and Five therefore provide a detailed investigation into some of the most noticeable gaps in our current knowledge of demography in this population of seals, and attempt to clarify the existing published disputes in this regard.

Chapter Six provides a more philosophical examination of the potential obstacles faced by researchers when using sophisticated analytical software, with a particular emphasis on capture-mark-recapture data and the software program MARK. I use an analysis aimed at identifying potential marker confusion (due to tag colour) in the Marion Island elephant seal population, to illustrate the point.

The Appendices of this thesis investigate various factors of broad relevance to both field methodology and their ecological interactions with elephant seal population demography research. Although I initiated the research pertaining to the appendices and contributed significantly to their current form, much of the analyses and thus lead authorship on Appendices 2 and 3 were contributed by collaborators as shown.

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CHAPTER TWO:

HOW TO WEIGH AN ELEPHANT SEAL WITH ONE FINGER: A SIMPLE THREE-DIMENSIONAL PHOTOGRAMMETRIC APPLICATION

de Bruyn et al. 2009

Abstract

Several studies have developed photogrammetric techniques for indirect mass estimation of seals. Unfortunately, these techniques are often narrowly delineated for specific field scenarios or species. Many require sophisticated, custom-designed equipment or analytical tools, limiting their applicability. We aimed to devise a photogrammetric technique for accurate volume / mass estimation of seals under a variety of field scenarios without manipulation of the animal and with minimal equipment. We use Photomodeler Pro® three-dimensional modelling software to estimate the mass of fifty-three weighed southern elephant seals, *Mirounga leonina*. The method is centred on animal volume estimation in relation to the three-dimensional area around it, rather than features of the animal itself, an approach that liberates limitations associated with earlier studies. No morphometric body measures are required for such volume / mass estimation. We offer predictive equations that allow high confidence in mass estimates relative to measured mass (95% confidence interval of mean deviation from measured mass from ±1.34 % to ±3.83 % depending on the field scenario). A single photographer with a measuring stick and non-customised digital photographic equipment can use this technique to determine the mass of an elephant seal anywhere in the field with the push of a button.

Introduction

Body size of vertebrates (including related characteristics such as body mass) is a central theme in studies investigating geographical scaling patterns, physiological, behavioural and life history parameters of individuals and populations (Peters 1983). Body mass estimation of terrestrial and marine mammal species are regularly based on scaling procedures of various body measurements (e.g. Bryden 1969; Christiansen 1999) and Trites and Pauly (1998) observed strong linearity when maximum body length of 17 marine mammals species were plotted against mean individual mass. The ubiquitous terrestrial phase of pinniped species and their cumbersome movement on land as compared with truly terrestrial large mammals, have prompted biologists to use pinnipeds (more so than other mammalian groups) as study subjects to attempt body mass predictions based on morphological features.

Given the scaling relationships between morphological measures and body size/mass, various photogrammetric techniques (the use of photographs to measure objects) have been used to determine diverse morphological measures of mammals, including shoulder height and back length of African elephants, *Loxodonta africana* (Hall-Martin and Rüther 1979; Schrader et al. 2006), dorsal fin analyses of killer whales, *Orcinus orca* (Keith et al. 2001), and baleen rack shape and size in bowhead whales, *Balaena mysticetus* (Lambertsen et al. 2005). In pinnipeds, Haley et al. (1991) initiated photogrammetric use for body mass estimation in northern elephant seals, *Mirounga angustirostris*, while Bell et al. (1997) applied a combined photogrammetric and morphometric technique of estimating body mass in southern elephant seals. However, the constraints under which current methods of photogrammetry can be used to accurately estimate seal mass are rigid. Animals have to be on a completely flat surface (e.g. hard/packed sandy beach), lying straight in ventral recumbency with no tolerance for movement, and the images captured when the animal has inhaled completely (Haley et al. 1991; Bell et al. 1997). The photographer is required to know the exact distance between the camera and the seal and scaling measure. More recently, Ireland et al. (2006) and Waite et al. (2007) made significant advances using new technology to estimate the masses of Weddell seals, *Leptonychotes weddellii*, and Steller sea lions, *Eumetopias jubatus*, respectively. These methods have increased the accuracy of mass estimation for the particular species but introduced (or maintained) various constraining field procedures, restricting their use in the field. The Ireland et al. (2006) method requires customised photographic equipment that is bulky and impractical in situations where the only method of traversing large distances between study subjects is by walking. Proffitt et al. (2008) successfully improved the photogrammetric mass estimation and confidence of the Ireland et al. (2006) procedure, by *post hoc* body form analysis using elliptical Fourier decomposition. However, the study did not simplify the field photographic component. The Waite et al. (2007) technique required sophisticated targeting on the seal and synchronized images from different angles to allow the three-dimensional modelling of the subjects and required best estimates to remain morphologically correlated. Thus, all these methods require physical contact with the animal to acquire a morphometric measure or to manipulate posture. Restricted accessibility to haul-out locations, uneven substrates at haul-out sites, adverse weather conditions, and the behaviour of wild seals render all these methods largely unsuitable for extensive and simple field implementation.

We report on a novel three-dimensional photogrammetric field technique for mass estimation of pinnipeds without many of the abovementioned constraints. This technique is based on a volumetric estimation method that requires only one photographer with a digital camera and a calibrated measuring stick in the field. The technique was developed with the logistical challenges of isolated study areas and with varying substrate topography, in mind. Additionally, analyses can be performed with a non-customised commercially available software package.

Methods

Study area

This study was conducted through several seasons between April 2006 and February 2008 at Antarctic-maritime Bouvetøya (BVT) (54°25’S, 03°20’E), Stranger Point on King George Island (KGI) in the South Shetlands (62°14’S, 58°40W) and Subantarctic Marion Island (MI) (46^{o}54’S, 37^{o}45’E) (Fig. 1.1). Beach topography varied considerably between the three localities and within each site, ranging from flat sandy or pebble strewn to heavily bouldered substrates, sometimes covered in kelp and/or snow and ice, i.e. heterogeneity in beach topography that severely negates the use of existing photogrammetric techniques.

Field techniques

Fifty-three southern elephant seals of both sexes and varying age classes (Table 2.1) were weighed and photographed according to the procedures set out below.

Table 2.1. Number of southern elephant seals, in each age - and sex class, included in this study. The mean body mass and range within each class are shown.

Sex	Age category	Age (years)	No. animals	Mean body mass - kg (range)
Male	Underyearling	<1	2	145 (140-149)
Male	Yearling	1	0	-
Male	Juvenile	2-3	12	314 (212-387)
Male	Subadult	4-5	11	443 (348-569)
Female	Underyearling	<1	0	-
Female	Yearling	1	2	166 (132-200)
Female	Juvenile	2	7	226 (163-269)
Female	Adult	>3	19	431 (295-636)
Total			*53*	*359 (132-636)*

Weighing procedure

Animals at MI and KGI were immobilised using an intramuscular dose of ketamine hydrochloride (2.4-6.2 mg kg^{-1} estimated body weight) (Bester 1988; also see Appendix 1), while animals at BVT were immobilised using an intravenous dose of zolazepam:tiletamine (1:1) (Zoletil®; ~0.5mg kg^{-1}) after temporary restraint of the seal using the canvas head-bag technique (McMahon et al. 2000). Animals were then weighed in either a net stretcher or broad strapping suspended from a load cell (different manufacturers depending on the location), attached to a block-and-tackle and suspended from either a steel, aluminium or carbon-fibre tripod. Seal mass (±0.5kg) was corrected in all cases for additional mass resulting from nets or strapping. Scales were calibrated with a known mass between weighings. Standard length measurements were taken for each animal while in ventral recumbency (Bonner and Laws 1993).

Photographic procedure

Following weighing, each animal was photographed between eight and ten times from several different angles and heights (Fig. 2.1a and 2.1b). The placement of camera stations (i.e. the approximate angle relative to the animal from which the photograph was taken) was roughly standardised (Fig. 2.1), but exact distances from the seal or measuring stick need not be known. A Canon EOS350D digital SLR

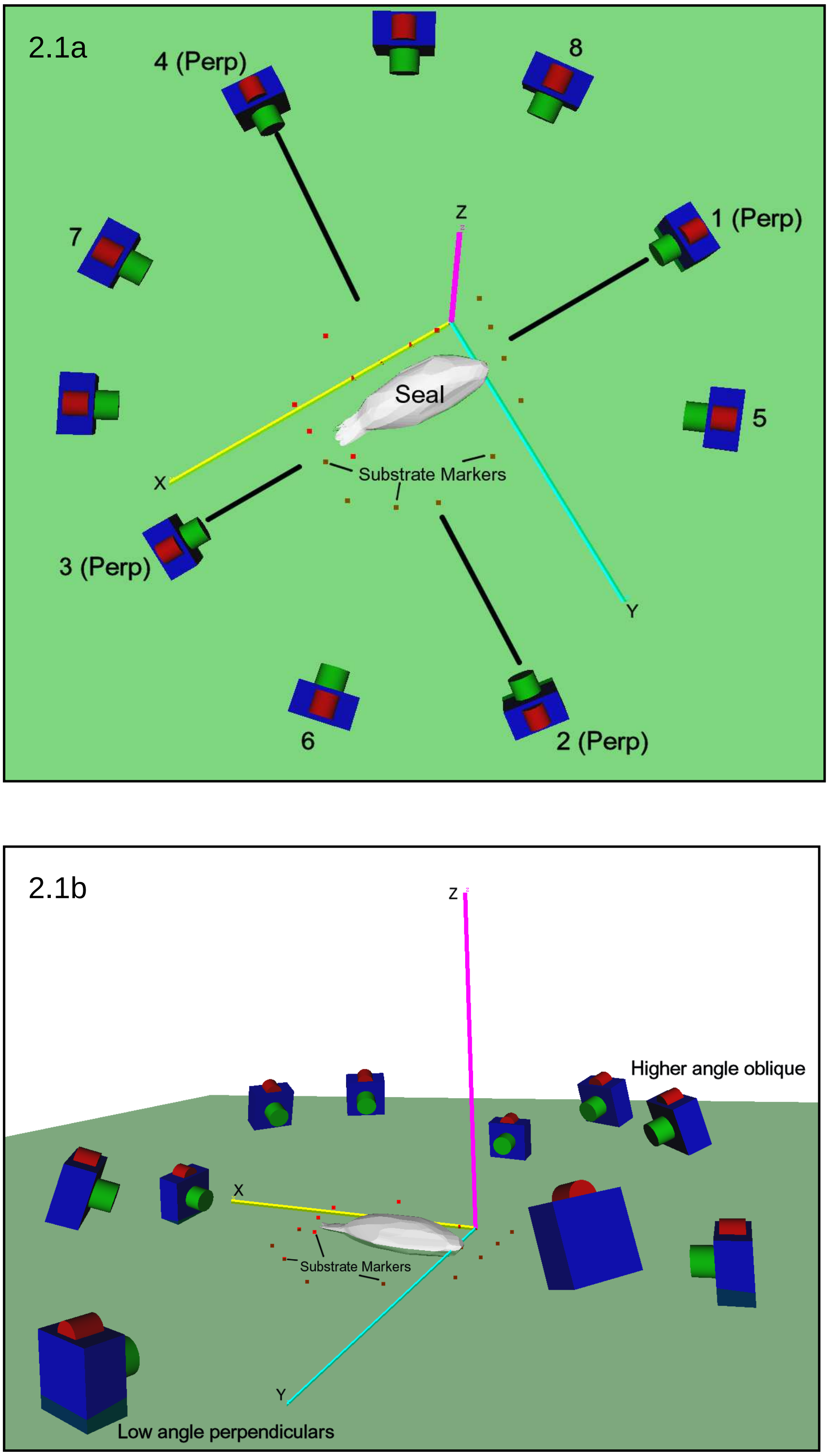

Fig. 2.1. The placement of camera stations (positions from where the photographs are taken) around the object to be modelled (2.1a - top view); and photographs should be taken at varying heights around the object (2.1b - side view). Note the placement of the low angle perpendicular photographs.

camera (high-resolution: 8-megapixels), with 18mm Canon lens was used for photography at MI and BVT, while a Samsung Digimax 201 compact digital camera (medium-resolution: 2-megapixels) at an EXIF focal length of 5.6mm was used at KGI. An independent project was done for each of the 53 seals and either one or the other camera was used per project. A single photographer circling the seal took the photographs. Miscellaneous objects (5 to 15; e.g. tags, tag applicators etc.) were randomly distributed on the substrate immediately around the seal as landscape/substrate markers (in addition to natural markers such as stones). Importantly, these markers remained unmoved during photography. A calibrated measuring stick 150cm in length, was placed somewhere amongst the markers to provide a scaling measure and also remained unmoved. The whole seal, markers and measuring stick were included in each photograph where the camera station allowed. Providing that the measuring stick/ each marker was entirely visible in at least three of the photographs in a project, the seal in the foreground obscuring markers and/or measuring stick behind it was acceptable. Given the objective of providing a photogrammetric method with tolerance for seals resting on a variety of substrates (for applicability in the natural scenario), the substrate on which the animal was resting was categorised as either even (flat) or uneven (rough). Even surfaces had no depressions or protuberances (rocks), and a flat plane with little or no curvature under the seal (e.g. a hard sandy - or finely pebbled beach). Uneven substrates had significant depressions or protuberances under the seal (such as a rocky/boulder beach, undulating moult wallow or deep kelp bed), which may displace or “swallow” some of its volume. On uneven substrates, the seal can thus be classified as not having a uniform planar surface where it’s body is in contact with the substrate. The body posture of seals was not manipulated for photographic purposes and subjects were left undisturbed to assume a position of choice after the weighing procedure.

Photogrammetric analyses

Volumetric estimation

Volumetric estimation procedures were performed using the commercially available three-dimensional (3-D) modelling software package, Photomodeler Pro® Version 6.2 (EOS Systems Inc., Vancouver, British Columbia). In an independent, stringent evaluation of this software, Deng and Faig (2001) confirmed the high level of accuracy in the creation of the relevant 3-D space, justifying its use especially for digital close-range (i.e. not remote sensing) photogrammetry. The initial step (prior to fieldwork) is to individually calibrate each camera (and relevant lens combination) using the procedure and test pattern provided by the software. The program requires calibration resulting in known focal length of the lens, the digitizing scale (the charge-coupled device - CCD - format size of a digital camera), the principal point (where the optical axis of the lens intersects the photograph) and parameters that describe distortion characteristics of the lens. Following camera calibration, the photographer need not know the distance from the object and each camera station can be randomly placed at various distances (and heights) around the object. This provides the option for using images from different non-identical cameras in one project provided each camera is calibrated (see Photomodeler Pro® help file). Calibration for each camera/lens combination occurs only once before its first use.

We initially attempted to create a 3-D model of each seal based on the technique used by Waite et al. (2007) for Steller sea lions whereby orientation points on the seal are cross-referenced between photographs to create a 3-D space. Our attempts at this method failed because, firstly, natural marks on seals are scarce and/or difficult to identify for cross-referencing between photographs, and secondly, seals (even when immobilised) move when breathing or otherwise, resulting in slight shifts of orientation points between photographs. To surmount this problem, initial 3-D model construction was shifted away from the seal and focussed on the inanimate elements of each photograph, the substrate landmarks. Points identified on substrate markers (natural or inserted) were then cross-referenced between photographs containing those points, to create a 3-D space within which to continue the model construction. On average, 22 (range 16-36) cross-reference points were used per individual project (e.g. Fig. 2.2) to orientate all photographs, although all points were not visible on all photographs in a project. The software requirements for maintaining minimum “residual error (RMS)” of each point (below 5.0; see Photomodeler Pro® help file) on each photograph were adhered to (see Graff and Gharib 2008, for details of accuracy in point based 3-D volumetric measurement systems). Once all photographs were successfully orientated based on the cross-referenced substrate points and an acceptable (RMS < 5.0) 3-D space created as a result, the scale measure was marked on this orientated substrate (Fig. 2.2). The object (seal) shape was subsequently modelled in this 3-D space using the “silhouette” method (Fig. 2.2) of object model construction (see Photomodeler Pro® help file). In the case of visual obstruction of a part of the seal, e.g. by rocks in the foreground of the photograph, the imaginary outline was followed. If >30% of the seal was obstructed from view, the photograph was discarded.

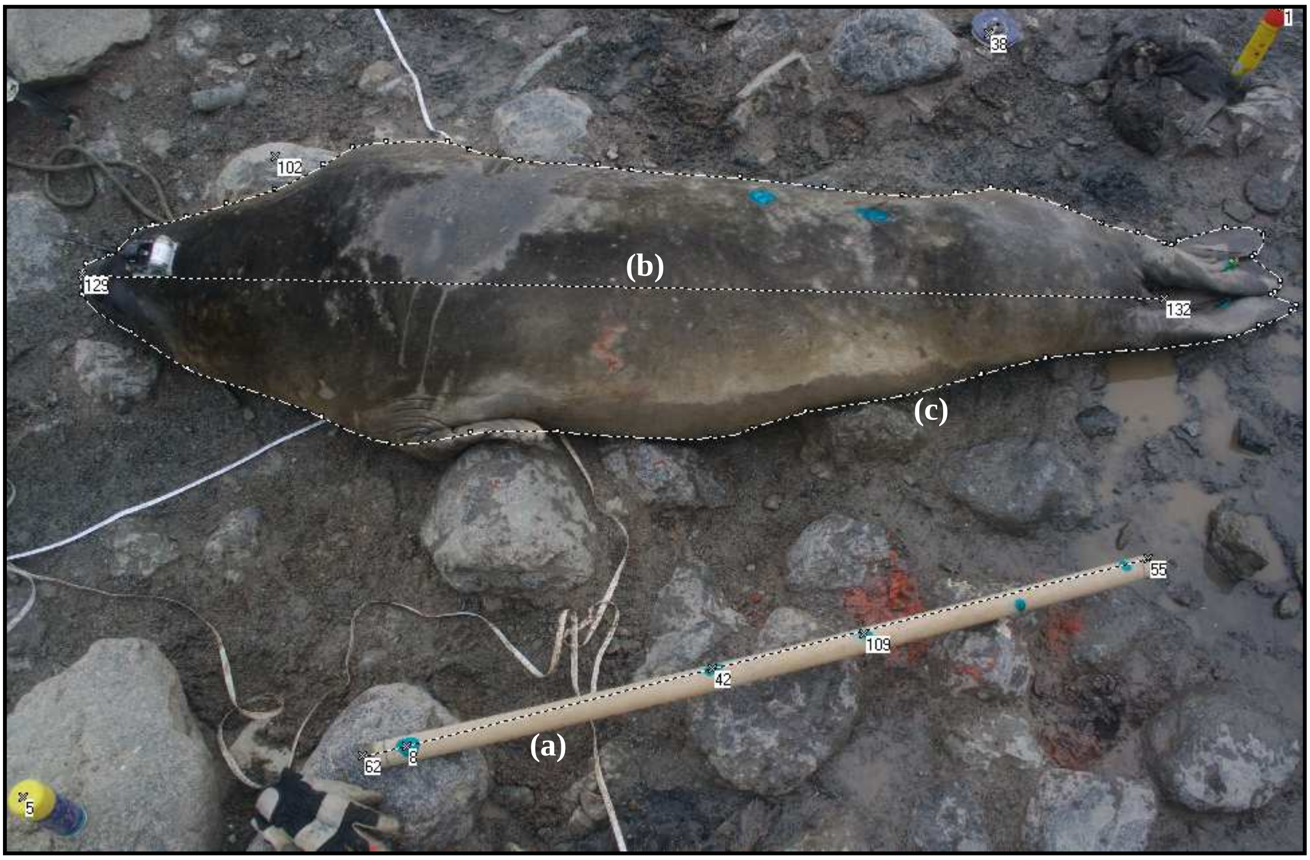

Fig. 2.2. An image of a southern elephant seal depicting the two scaling measures used separately for calculation of volume: (a) measuring stick or (b) standard length. Note the silhouette line (c) traced on the outline of the seal, which has been cross-referenced with similar silhouettes traced around the same animal on other photographs. Substrate markers (randomly numbered) have been used to create a three-dimensional space, by cross-referencing these points with the same points on other photographs.

Seal silhouettes were sequentially traced for each photograph (one silhouette *per* photograph) and volumetric estimates were obtained after the addition of each silhouette, starting at 3 silhouettes (the minimum needed to create a shape) through to 10 silhouettes, to test if volume estimates reached an asymptote after the addition of a specific number of photographs (camera stations) to the project. The Photomodeler Pro® measuring tool was used to assign a scaling measure to the project based on the measuring stick in the photographs. To test if morphometric measures of the seal should be used as a scaling measure to improve ultimate estimates (see Waite et al. 2007), we marked the standard length of the seal on the photographs, assigned this as the scaling measure for the model, and compared the derived volumetric estimate with that gained from using the measuring stick in the image. Standard-length-scaled and measuring-stick-scaled volume estimates were compared for all 53 projects.

We extended/constricted some silhouettes in a project incorrectly (but realistically) to mimic head, flipper or breathing related movement between photographs and recalculated the volume estimates. Front-flippers were not included in the silhouette outline but hind-flippers were. Front-flippers are easy to exclude by following the bodyline of the seal. Head and hind-flipper movement of up to 45^{o} (angle between two head positions in the same project) in any direction was mimicked, while some full inhalation silhouettes and some complete exhalation silhouettes were modelled in the same project. Totally immobile - and "movement related" volume estimates were compared for 20 projects.

To test Photomodeler Pro®'s specification that projects with overall project RMS < 5.0 are accurate, we re-orientated ten animals three times as separate projects to test whether variation in substrate cross-referencing quality (that may be caused by different users for example) caused variation in ultimate volume estimates.

Mass estimation

The volume estimates of each object gained from Photomodeler Pro® were separately multiplied by two different density values to calculate the mass of each seal. Firstly, the annual haul-out cycle of southern elephant seals (Kirkman et al. 2001, 2003, 2004) and its effect on body composition (blubber vs. lean-mass) was considered. Mean percentage body blubber content for seals of different sexes and ages (Bryden 1972; Slip et al. 1992; Carlini et al. 1999, 2005; Field et al. 2005) were converted into a blubber to lean-mass density ratio based on the densities of blubber ($0.95 kgm^{-3}$; Gales and Burton 1987) and lean-mass ($1.10\ kgm^{-3}$; Le Boeuf et al. 2000), and this ratio applied to the volumetric estimates to obtain estimated mass. Secondly, a density of $1.01\ kgm^{-3}$, the mean ($\pm 0.04\ kgm^{-3}$) total-body density for healthy mammals regardless of total body fat content (Durnin and Womersley 1974;

Wang et al. 1999) was used for mass estimation of all animals. Use of the latter broadly applicable density thus precluded judgement of the body condition of the seals.

Data analysis

The deviation in predicted mass to measured body mass (% under- or overestimate, hereafter called percentage error) was calculated for all projects and was used to evaluate predicted mass estimates. Firstly, we determined the minimum number of photographs that a project should use by comparing volumetric estimates from projects spanning three to ten photographs. The first four photographs (1 to 4) used were always those at perpendicular angles to the subject (Fig. 2.1a), and further photographs from remaining camera stations (Fig. 2.1a) were sequentially added to each project in the same order as was done for other projects. Then we tested for differences in percentage error from projects using a measuring stick or a standard length morpho-measure scale (Fig. 2.2). We also compared the percentage error from different cameras, although we were not able to compare the effect of different cameras on the same subject. Since camera differences were non-significant, and the use of a measuring stick resulted in significantly lower deviation from measured mass (see results), we grouped data from all study sites and used data from measuring-stick-scaled projects only in subsequent analyses. We compared the percentage error for all projects based on a mean density of 1.01 kgm^{-3} and on a blubber-to-lean-mass density ratio as predicted by haul-out type. Using the best volume to mass density conversion factor, we computed the mean effect of missing a single perpendicular photograph, or missing photographs encompassing an entire side view (180°), compared to the full view model by deleting relevant photos from full view projects. We fitted a general linear model to evaluate the effects of animal sex, age class (juvenile, subadult, adult), haul-out type (winter, pre-moult, mid-moult, post-moult), head movement during photographs (present or absent), and substrate (even or uneven) on predicted mass estimates. We constructed a single global main effects model relating one continuous predictor variable to multiple (all) classification predictor variables. We did not test for interactions between explanatory variables, which would have been the first term to eliminate in a model selection process, and were interested in the importance of variables only, not their model estimates. All analyses were performed using STATISTICA 7.0 (StatSoft; Oklahoma, USA), except the linear model that was fitted in SAS 9.1 (SAS Institute; Cary, NC). Data were tested for normality using the Shapiro-Wilk W test. The deviation in predicted mass to measured mass (percentage error) is presented as mean ± 95% CI and probability values are considered statistically significant at $p \leq 0.05$. Proportional data were arcsine transformed where relevant.

Results

Our results indicate that confident (percentage error 95% CI from ±1.34 % to ±3.83 % depending on the field scenario) mass estimates relative to measured mass can be obtained with the use of this method. A mean of 6 minutes (range: 2 to 10 min) in field effort was required for photography of each of the 53 animals. On average, 50 minutes (range: 20 to 210 min) were required by a user to create a 3-D modelled space and object shape (i.e. one project).

Volumetric estimation

The same project cross-referenced anew (three repeats) never provided identical project RMS values. However, in maintaining RMS <5.0 for each of the three projects, ultimate volumetric estimates of the seal shape between the three iterations varied only by a third of a percent (range: 0.02% - 0.28%). Mean overall project RMS for individual projects (n = 53) was 1.518 pixel units (range: 0.774 - 3.576).

The "totally immobile" and mimicked "movement related" volume estimates tested in 20 projects were identical. If the bulk of the body shifted more than ~15 cm in any direction between photographs, the resulting 3-D model was visibly affected, resulting in "tolerance violation" (see Photomodeler Pro® help file) and the software rendered the volume calculation unsolvable.

Project volume estimates improved significantly with every additional silhouette (after three) included in the model (dependent t-test, from 3 to 8 photographs $p < 0.001$). An asymptote was reached at eight photographs ($t_{(8\text{-}9\ \text{photographs})} = 0.35$, $p = 0.72$; $t_{(8\text{-}10\ \text{photographs})} = -1.10$, $p = 0.28$) (Fig. 2.3). Adding additional photographs to an eight-image project (mean project silhouette volume

0.355 ± 0.033 m^3) therefore did not significantly improve volume estimates (mean project silhouette volume for ten-image project 0.352 ± 0.033 m^3).

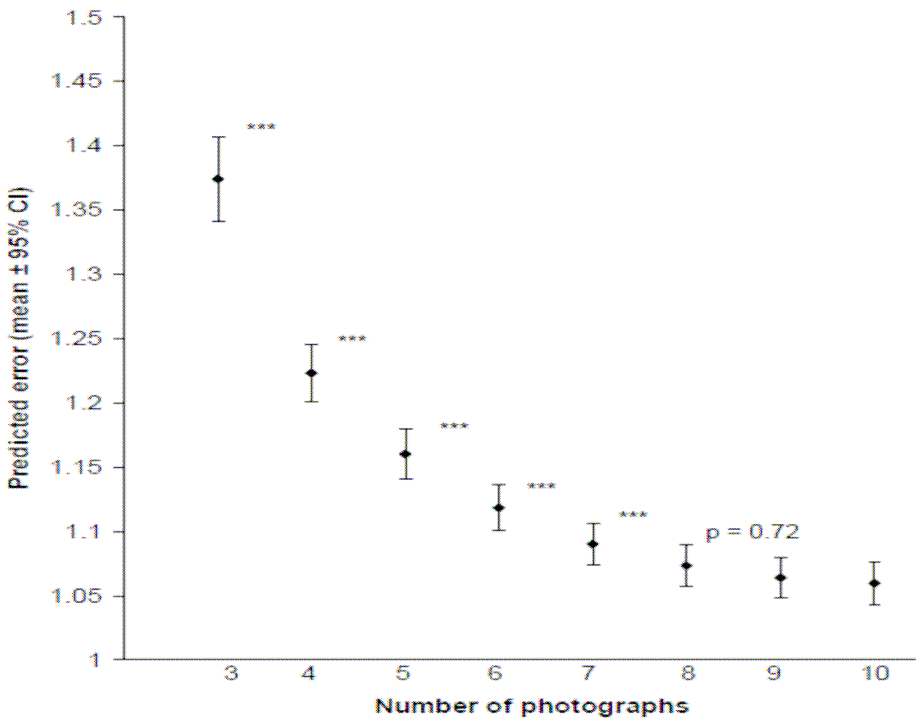

Fig. 2.3. Number of cross-referenced silhouettes (1 silhouette per photograph) required in Photomodeler Pro® before an asymptote of volumetric estimation was approached. Volumetric accuracy increased significantly with addition of every silhouette up to 8 photographs in a project. ***Significant decrease in volumetric predicted error ($p < 0.001$).

Mass estimation

Mass estimates of full view projects based on a measuring stick had less variation and were closer to measured mass (9.71 ± 1.27%) than those based on morphometric standard length measurements (12.73 ± 2.30%; dependent t-test, $t = -2.78$, $p < 0.01$). The two different cameras used had similar percentage error estimates (Canon 8.60 ± 2.91% and Samsung 10.10 ± 1.37%, independent t-test, $t_{(104)} = -1.03$, $p = 0.31$). Model accuracy decreased significantly when the ratio density method was used compared to estimates based on a mean density of 1.01 kgm^{-3} (dependent t-test $t_{(52)} = -36.48$ $p < 0.001$). The full view model consistently overestimated measured mass (6.59 ± 1.52%). Overestimates of predicted mass increased further when a single perpendicular angle or an entire side view were deleted from projects, with the percentage error significantly higher than for the full model (repeated measures ANOVA, $F_{(2,70)} = 203.46$, $p < 0.001$) for both perpendicular (9.36 ± 2.09%) and missing side view (20.83 ± 2.72%) models

(Tukey's HSD *post hoc* test for unequal sample sizes; $p < 0.01$). The variables included in the linear model explained little of the remaining variation in photogrammetric mass estimates ($F_{(5,\,41)} = 4.69$, $p = 0.018$, $R^2 = 0.36$), with substrate type the only significant determinant (beta = -8.25, $F = 17.78$, $p < 0.001$). Even substrates resulted in an overestimate of predicted mass with narrow confidence intervals (8.54 ± 1.34%), while uneven substrates provided estimates close to the measured mass (0.57 ± 2.69%), albeit with greater variance.

Predictive equations

We applied equations to the predicted mass data (based on the mean percentage error) to adjust the mean overestimation of measured mass as estimated by this method (Table 2. 2). All equations are dependent on the use of a measuring stick for volumetric scaling in the project and a mean density volumetric conversion factor of 1.01 kgm^{-3}. R^2 values were derived by plotting measured mass, against predicted mass and corrected mass using the appropriate equations (Fig. 2.4).

Table 2.2. Predictive equations to approximate body mass of southern elephant seals. The full view model depicts a minimum of 8 photographs including all perpendiculars and all sides of the object (Fig. 2.1). R^2 values are the resultant linear regression fit of measured mass to predicted body mass for this dataset.

Model	**Equation** [a]	***N***	***R^2***
Even substrates:			
Full view	PBM = ME – [ME x (0.085 ± 0.013)]	40	0.98
Missing one perpendicular	PBM = ME – [ME x (0.108 ± 0.019)]	31	0.97
Missing an entire side view	PBM = ME – [ME x (0.244 ± 0.026)]	40	0.96
Uneven substrates:			
Full view	PBM = ME – [ME x (0.006 ± 0.027)]	13	0.98
Missing one perpendicular	PBM = ME – [ME x (0.004 ± 0.038)]	5	0.97
Missing an entire side view	PBM = ME – [ME x (0.099 ± 0.034)]	13	0.97

[a] PBM - Predicted body mass (kg)
ME - Mass estimate from photogrammetric volume (kg)

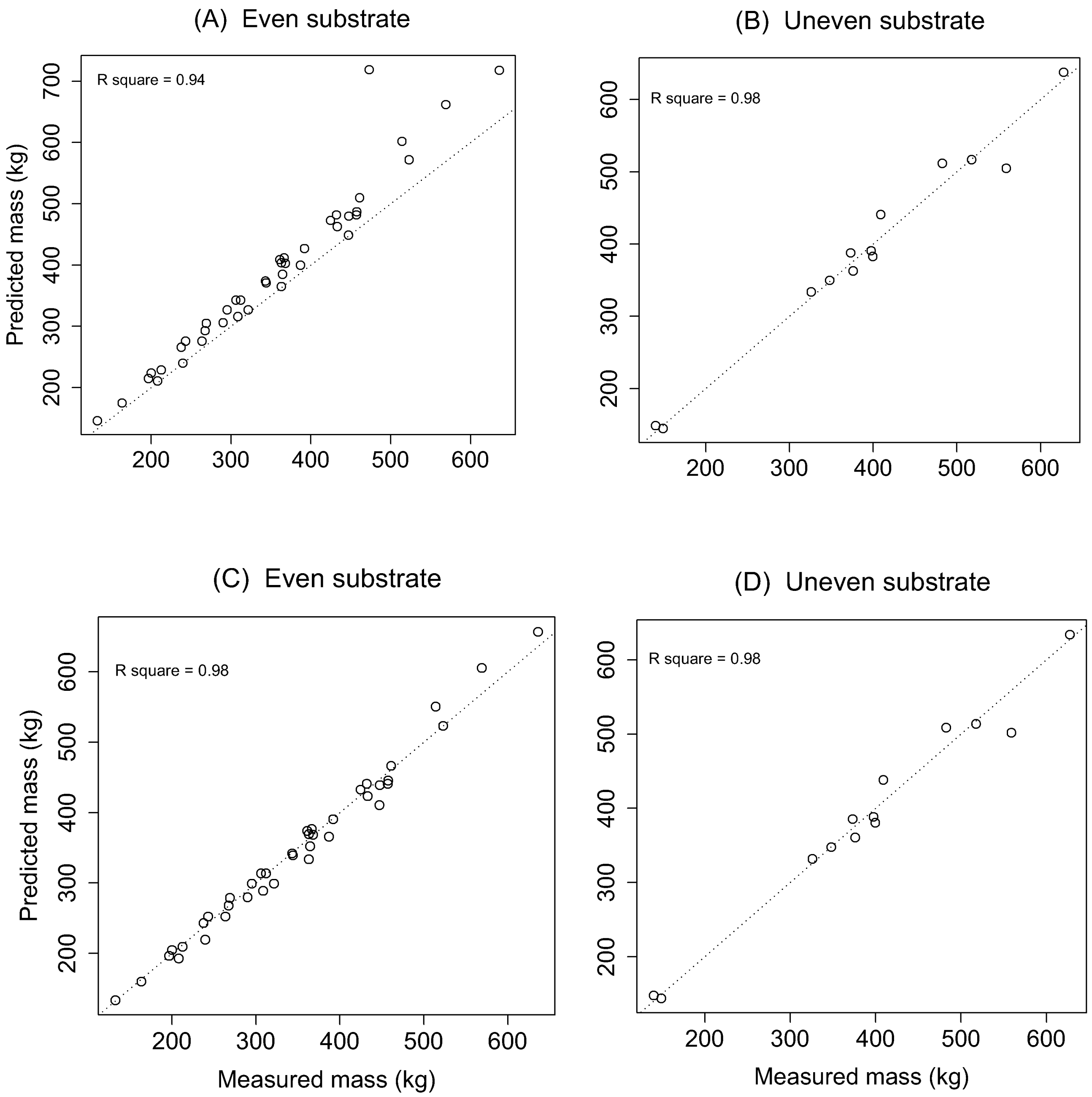

Fig. 2.4. Regression of predicted body mass against measured body mass for southern elephant seals on even and uneven substrates. A and B represent the predicted mass values obtained from full view photogrammetric projects, while C and D are the predicted mass estimates multiplied by the appropriate correction factors given in Table 2.2. The dotted line represents the true regression line (intercept = 0, slope = 1).

Discussion

This photogrammetric mass estimation method centres on the accurate estimation of the volume of an object within a 3-D space orientated by cross-referencing of inanimate points surrounding this object. This approach ensures that the animate object to be modelled (seals in our case) is not dependent on features of itself, but rather on the more stable substrate to create an accurate 3-D space. This liberates many constraints associated with modelling of an object (Proffitt et al. 2007, 2008), such as absolute immobility of the object, clearly recognisable 'landmarks' or measures on the object (morphometrics), and specific object postures or shapes (Haley et al. 1991; Bell et al. 1997; Ireland et al. 2006; Waite et al. 2007). In so doing, this 3-D modelling procedure addresses our objective for simple photography of seals (without physical contact) on a variety of substrates without the need for sophisticated, bulky or custom designed equipment. Because cross-referenced silhouettes do not depend on accuracy measures of the silhouetted object, but rather on the surrounding substrate markers, slight movement of the object (and thus the marked silhouette), or object complexity, has a limited influence on ultimate project accuracy and the volume estimate. Thus, although an animal needs to be stationary, our results suggest some tolerance for movement (particularly of head or appendages). Additionally, this method diverges from the morphometric-to-body-mass scaling procedures used to date. Firstly, it removes the constraint to immobilize and physically measure study subjects. It can therefore be used on stationary seals without the need to handle seals. Secondly, this method is not restricted to the scaling relationships of a specific species. In light thereof, it seems probable to determine the volume of a large mammal regardless of the species or surroundings, and to calculate the mass of a particular animal based on the narrow total-body density range applicable to mammals (Durnin and Womersley 1974; Wang et al. 1999). However, our results are based only on southern elephant seals, and while the physics and functionality of the software and method suggests its applicability to other mammalian groups, its accuracy therein remain to be confirmed.

The immobility of the study subject when using this method is a by-product of the single photographers' need to circle the animal (for field application), however the software provides the option for the processing of photographs depicting the same object but produced by different calibrated cameras. In projects where seals rested on highly uniform substrates (e.g. snow, sand), the addition of non-natural substrate markers (e.g. unique, coloured marbles) around the seal reduced analysis time considerably (less time required than to search for natural markers). This is superfluous for model construction when adequate natural markers are present.

Three iterations of 3-D space construction for the same project did not produce identical results due to the difficulty (even for the same user) of placing a mark on exactly the same pixel in an image in three exclusive attempts. However, ultimate volumetric estimates of the seal shape between the three iterations (e.g. different users) remained negligible if software stipulations were adhered to (i.e. RMS <5.0). No significant difference between the use of a medium – or high-resolution digital camera was evident in estimates. Consequently, one is not obliged to purchase expensive or sophisticated digital camera equipment to apply this method.

High - and low angle photographs from camera stations around the subject (top views are especially useful, albeit not crucial) are critical for accurate model construction (PJNdB personal observation). This is due to the silhouette method simply calculating the shape and size of an object from the silhouette projection algorithm when the silhouette is referenced on three or more orientated photographs. This effectively means that a missing side view results in an overestimation of the extent of the object on the opposite side of the missing camera stations because there are not sufficiently angled camera stations to allow the software to trim the model. This silhouette projection algorithm is also likely the cause for the difference in mass estimates between animals on even and uneven substrates. Because photographs of the object cannot be captured from a camera station exactly at / or lower than ground level, the 3-D model based on silhouettes result in a convex, rather than planar, lower surface for the object. The volume of an animal resting on an uneven substrate where some of its volume may in reality be “swallowed” by a depression under it would therefore be more correctly modelled as having a convex lower surface. The greater variance around estimates for uneven surfaces result from not every animal on an uneven surface having a completely convex lower surface, (e.g. sometimes it may be partially convex and partially concave due to uneven terrain). An animal resting on an even surface would in reality have a planar lower surface but that would still be modelled as convex, resulting in the consistent overestimates (but with greater confidence) reported here. We provide predictive equations for field scenarios where an incomplete set of photographs are available (missing a side view due to a large boulder preventing camera stations on a specific side for example) for subjects resting on even or uneven substrates, but caution their use for high accuracy mass estimation.

An added advantage of using the substrate point referenced 3-D space method (this study) is that a measuring stick can be photographed on the substrate where the animal was situated, *after* its departure. These photographs are then orientated with those where the subject is present to provide a scale to the project. Alternatively, a unique feature on the substrate can be measured after photographs were taken and included as the scaling measure. The significantly poorer performance of a morphometric measure as compared with an inanimate measure in the project results from the inability to accurately mark standard length on animals in the photographs. This can be due to some points of the animal (such as tail tip) not being visible on photographs, movement of the head resulting in error when the apex of the nose is cross-referenced, or the posture of the animal.

The technique can greatly assist longitudinal studies (see Chapter 3 - de Bruyn et al. 2008) that would traditionally have required reweighing of marked animals (Fedak and Anderson 1987). It reduces limitations for mass estimation under the following requirements: (1) Use a calibrated digital camera, (2) Take at least eight photographs around the stationary animal (Fig. 2.1) and include sufficient substrate in each photograph to facilitate point identification, (3) Include a measuring stick (preferably greater than 1.5m in length for large mammals) in at least three of the eight photographs.

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