Inter-population craniometrics of adult male Subantarctic fur seals (*Arctocephalus tropicalis*)

Inter-population craniometrics of adult male Subantarctic fur seals (*Arctocephalus tropicalis*)

By

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Submitted in partial fulfilment of the requirements for the degree of

M.Sc (Zoology)

In the

Department of Zoology and Entomology

Faculty of Natural and Agricultural Sciences

University of Pretoria

Pretoria

South Africa

March 2014

Declaration:

I, **Moleseng Claude Moshobane** declare that the dissertation, which I hereby submit for the degree **M.Sc. Zoology** at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature:……

Date: ……

Summary

Inter-population craniometrics of adult male Subantarctic fur seals (*Arctocephalus tropicalis*)

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Abstract

Craniometrics is a very reliable and effective tool for studying the difference in animal morphology. Previously, traditional craniometrics were conducted with the aid of calipers in two dimensional format (2D). Such discounting of actual three-dimensional 3D form may result in loss of some relevant and critical information leading to compromised and unreliable results for studies such as population variation analysis of morphology. The employment of 3D photogrammetry allows a close to complete representation of the physical dimensions of a specimen. The use of photogrammetry in mammalogy concentrated on measuring of body size/mass, but little has been done on animal skull delineation through photogrammetry.

This dissertation describes advances in morphometrics and 3D photogrammetry application in craniometrics, investigates the craniometric variation between closely related species (*Arctocephalus gazella* and *A. tropicalis*), and *A. tropicalis* interpopulation craniometrics between two geographically distinct populations, at Marion Island and Gough Island, using Photomodeler Scanner® (PMSc®) three-dimensional (3D) modelling software to produce accurate, high resolution 3D skull models.

A total of 117 3D models were created from adult male fur seal crania, and 16 traditional measurements recorded, using specimens archived at the Port Elizabeth Museum, Bayworld, South Africa. Sixteen linear measurements, (8 caliper

recordings and 8 3D recordings) were used for PMSc® methodology testing, 16 (*A. gazella* n= 8 and *A. tropicalis* n= 8) used for species cranial comparison and 85 (Marion Island n= 54 and Gough Island n= 31) used for interpopulation variation. The craniometric variations were analysed using the Statistica® v11 software package, StatSoft, Inc. The comparison between linear traditional caliper cranial measurements and 3D measurements produced significantly similar results, attesting to the accuracy of the PMSc® 3D model production. Photomodeler Scanner® therefore produces accurate and high resolution 3D models of skulls which allow 3D measurements. I predicted that PMSc® would detect the existing significant differences between the skulls of adult male *A. gazella* and *A. tropicalis* and modelled and compared their 3D models, and I further predicted that PMSc® would detect any existing differences between the skulls of *A. tropicalis* from Gough and Marion islands by comparison of their 3D models. The Gough Island and Marion Island *A. tropicalis* populations could not be discriminated based on linear 3D cranial measurements.

I conclude that PMSc® is a reliable and effective tool for accurate and high resolution 3D modelling. The present study confirms previous findings and contributes additional evidence that suggests that adult *A. tropicalis* males from Gough Island and Marion Island cannot be discriminated based on linear measurements of craniometrics, and deviates from the Bergmanian rule as applied to large mammals. The present study, however, makes several noteworthy contributions to the use of PMSc® and 3D modelling in morphometrics. Taken together, these findings suggest a role for PMSc® 3D modelling in promoting accurate digitization of museum specimens and creation of online museum libraries. This research will serve as a baseline for future studies and usefulness of PMSc® in 3D morpho-volumetric measurements.

Key words:

Digital Morphometrics, Cranial Morphology, Subantarctic Fur Seal, Marion Island, Gough Island, Photogrammetry, 3D Modelling, Geographical Variation, Photomodeler Scanner®.

Acknowledgements

First and foremost I offer my sincerest gratitude to my supervisor, Prof Marthán Bester who has supported me throughout my dissertation with his patience and knowledge whilst allowing me the room to work in my own way. I attribute the level of my Masters degree to his encouragement and effort and without him this dissertation, too, would not have been completed or written. One simply could not wish for a better or friendlier supervisor.

I am greatly indebted to Dr Nico de Bruyn for the support he has extended to me throughout my work towards this dissertation, and for his informed guidance and advice. Whether my conundrum concerned something as minor as what classes to take, or something as significant as the wisdom of accepting a job offer, Dr de Bruyn always offered me good advice and brought previously unrecognized aspects of each situation to my attention. It was through him that I learned of the job opening at Bell Labs.

I also owe my deepest gratitude to Bayworld staff members. I would like to mention Dr Greg Hofmeyr, who patiently helped with the sampling experimentation in the Port Elizabeth Museum at Bayworld. I would also like to thank the persons who were responsible for the collection and preparation of the skulls, both at Marion and Gough islands.

I also extend my sincere gratitude to Dr Priit Kilgals and Patric Abila who, when I had only the vaguest idea of what statistical analysis was required, but was curious to learn more, gave me the opportunity to learn how to use statistical software and offered me encouragement, and took the time to explain the various nuances of the different statistical methodologies. Prof Susan Dippenaar has had a significant and invaluable positive influence on my development through her role as mentor.

My thanks also go to Martin Postma, Mia Wege, Mashudu Phalanndwa, who wholeheartedly welcomed me to the University of Pretoria and never tired of answering my questions. In my daily work I have been blessed with a friendly and

cheerful group of fellow students. Just to mention a few: Dr Marck Matlabyane, Mr Oscar Mohale, Admire Gamuchirai Madaure, Jeremiah Letsie, Elijah Chauke, Caleb Mabasa, Kgakantsho Boshielo, Lindoguhle Mathebula and Bongani Mshoba.

This dissertation is dedicated to my mother Tinny Nthlanngwe Moshobane, and my grandmother Moyahabo Annah Moshobane who have always supported me in my endeavours, always given me the strength and encouragement to follow my dreams, and have never left me in doubt of their love for me.

Disclaimer

Chapters within this dissertation have been structured in a scientific journal format. Thus has resulted in some overlap and repetition of methods used and I apologise for that.

Table of Contents

CHAPTER 1

General Introduction

CHAPTER 2

Assessing 3-D photogrammetry techniques in craniometrics

CHAPTER 3

Photogrammetric comparisons of adult male fur seal (*Arctocephalus gazella & A. tropicalis*) skulls

CHAPTER 4

Inter-population craniometrics of adult male Subantarctic fur seals (*Arctocephalus tropicalis*)

CHAPTER 5

General conclusion

APPENDIX A

List of tables

List of Figures

Manuscripts

Chapters 2, 3 & 4 in this dissertation were prepared for publication as separate manuscripts. Thus, the reader will find a fair amount of repetition, especially in the methods and material sections, for which I apologise.

Morphometrics Revolution: 3D Photomodeling in Craniometrics. MC Moshobane, PJ.N de Bruyn, MN. Bester

Prepared for: *Methods in Ecology and Evolution*

CHAPTER 1

General Introduction

Geographic Variation

Marine mammals, such as pinnipeds (Bester and Van Jaarsveld 1994; Brunner 1998a; Brunner 1998b; Brunner 1998d; Brunner 2002), dolphins (Rice 1998) as well as terrestrial mammals such as shrews (Poroshin et al. 2010) and deer (Langvatn and Albon 1986) show geographical morphological variability. These variations are directly related to their varying environments (Poroshin et al. 2010). According to Hutchinson (1957), the morphology may be affected by both abiotic (e.g. climate) and biotic factors (e.g. food availability) but this does not imply negligible influence of intrinsic factors such as genetics. The ecophenotypic and evolutionary responses to changing environments affect different populations of different species in a distinct way (Slater et al. 2009; Poroshin et al. 2010). For example, both cold and warm temperatures drive skull shape and size changes in common shrews (Poroshin et al. 2010). Several studies on different animal species support the existence of geographic variation in craniometrics (Knouft 2004; Endo et al. 2004; Bull 2006; Yom-Tov and Geffen 2006; Lahann et al. 2006; Ravosa 2007; Nygren et al. 2008). In addition, Bergmann's Rule states that "variation in body size within a species may occur due to climate differences - individuals from colder climates tend to be larger in size than those from warmer climates"(Bergmann 1847).

Bergman's rule applies to several groups of animals including protozoans, nematodes, insects, amphibians, fish, birds and reptiles (James 1970; McNab 1971; Voorhies 1996; Ashton et al. 2000; Ashton 2002a; Brunner 2002; Smith et al. 2002; Ashton 2002b; Yom-Tov et al. 2002; Ashton et al. 2003; Freckleton et al. 2003; Meiri and Dayan 2003; Blackburn and Hawkins 2004; Soobramoney et al. 2005; Lahann et al. 2006; McNab 2010). However, temporal and spatial sampling in some of these studies was limited and thus inconclusive. Furthermore, exceptions to this rule do occur, for example, minks do not adhere to this rule (Stevens and Kennedy 2006). These deviations from Bergman's Rule may be attributed to small differences in latitude between study sites (Stevens and Kennedy 2006) or the focus on body size,

a trait that is prone to being affected by many environmental and intrinsic factors (James 1970; Yom-Tov and Geffen 2006). The explanation for the Bergmanian thermoregulatory mechanism is that it is advantageous for heat retention per unit mass in large animals because of their lower surface to volume ratio (Mayr 1963). However, another mechanism apart from a thermoregulatory one suggested to account for latitudinal size clines is the primary productivity, heat load and seasonality (James 1970; Calder 1984). Thus the body size may be affected by any one of these factors (Yom-tov et al. 2003).

Craniometrics

Craniometry is the scientific measurement of cranial features which is of ancient origin and practiced from the early 19th century. It is widely applied in various craniology studies, both in anthropology and animals (King 1959; Wallace 1974; McHenry 1975; Zegura 1975; Schulter 1976; Smith 1976; Kerley and Robinson 1987; Gauthier et al. 2003). Marine animals can be difficult to study due to the inaccessibility of the marine environment and in studies of marine mammal morphometrics, skeletal remains such as skulls are used (Stewardson et al. 2008). Due to their robustness, remains of marine mammal skulls are commonly found (Stewardson et al. 2008) and archived in natural history museums. The adaptive and evolutionary significance of skull morphology divergence has previously been emphasized (Lu 2003). The comparison of the skull growth patterns between animals that are subject to different selection pressures as juveniles is particularly helpful (Lu 2003), because post natal skull ontogeny is subject to several environmental factors (Calder 1974; Wigginton and Dobson 1999). Hence skull ontogeny aids in understanding not only geographical variations in populations' phenotypes, but also their life history strategies and evolutionary changes (Lu 2003). Geographic morphological variations in populations may produce a basis for the studies on population changes, as well as for testing the hypothesis in evolutionary biology (Fornel et al. 2010) that populations tend to develop varying traits from the founder population through time.

Craniometric data is very reliable as it is consistent with genetic data (Fornel et al. 2010). The variations tend to occur in the chromosomal diploid number along the species' geographical localities (Fornel et al. 2010). Therefore skull morphometrics is

appropriate for phylogenetic reconstruction and population variation studies (Mazák 2010). Intraspecific morphological differences may provide the first evidence of ongoing differentiation processes (Fornel et al. 2010), and partially due to its utility for revealing the adaptive divergence within the species (Futuyma 1998). Other top predators such as lions show variation in skull morphology throughout their geographic range (Mazák 2010). Christiansen (2007) proposed that carnivore skulls differ extensively between different species and suggested that varied feeding capabilities, particularly to produce force and to uphold prey loads, are responsible for these differences (Wroe et al. 2005; 2007). Wroe et al. (2005) supported these hypotheses in their study on muscle cross-sectional area and leverage estimates of the extinct saber-toothed cat *Smilodon fatalis,* by demonstrating the muscular coordination in the exertion of force. Three-dimensional (3-D) computer simulation of the feeding behaviour in marsupial and placental lions also showed that biting force is directly related to the muscles in the neck region and thus variation in the skull morphology (Wroe 2008). Three-dimensional photogrammetry was also successfully applied on Galapagos tortoises carapaces (Chiari and Claude 2011).

Several studies investigated the presence of variation in skull morphology of different fur seal species (Kerley and Robinson 1987; Brunner 1998d; Kerley et al. 2000; Brunner 2002; Brunner et al. 2002; Brunner 2004; Molina-Schiller and Pinedo 2004; Sanfelice and Freitas 2008; de Oliveira et al. 2009; Slater et al. 2009). Most focussed on detecting differences between closely related species or between males and females. However, for a comprehensive understanding of the population dynamics of a given species it is vital to study the interpopulation craniometric differences of that species (Brunner et al. 2002) as various environmental conditions may perpetuate differentiation in various directions. The presence of the on-going population differentiation through time, might be revealed by interpopulation studies or possibilities of interpopulation breeding (Calder 1984; Wigginton and Dobson 1999). Alt et al. (1997) also suggested that craniometrics can yield valuable information on intra-population variability and that the use of craniometrics is reliable because it is seldom affected by abundance or scarcity of food in a given season. However, most of these craniometric studies used traditional methods (Drehmer and Ferigolo 1977; Kerley and Robinson 1987; Ansorge 1992; Brunner 1998a; Brunner 1998b; Brunner 1998c; Kerley et al. 2000; Brunner 2002; Brunner et al. 2002;

Molina-Schiller and Pinedo 2004; Sanfelice and Freitas 2008; de Oliveira et al. 2009) where instruments such as dial-, vernier- and digital callipers and measuring rulers were used. As cranial size and shape are strongly controlled by genetic mechanisms (Manfredi et al. 1997; Johannsdottir et al. 2005), most craniometric studies using traditional methods could not assign parameters such as volume or shape quantitatively. Photogrammetry therefore promises to be a more reliable tool for this type of undertaking.

Photogrammetry

Photogrammetry, the science of making measurements from photographs, is now a well-established technique used in a wide range of fields including architecture, art preservation, forensics, geology, agriculture, medicine, and mapping (Baker 1960; Walford 2008). In biological research, biological specimens were represented in 2D form, (Rohlf and Slice 1990; Rohlf 2000), and that wrongly implied that the 3rd dimension has no special biological meaning (Zelditch et al. 2004). The employment of 3D photogrammetry allows a more complete biological representation of the object of interest (Pavlinov 2000). Much work on the use of photogrammetry in mammalogy concentrated on measuring of body size/mass e.g. Haley et al. (1991), Modig (1995), de Bruyn et al. (2009), although several studies have assessed other morpho-characteristics (Jordan et al. 2001; Tasdemir et al. 2011). In human medicine some studies focused on maxillofacial surgery (Kau et al. 2007; Jayaratne et al. 2010), craniofacial shape (Douglas 2004; Weinberg et al. 2008), facial delineation (Douglas and Mutsvangwa 2010) and joints and skeletal analysis (Kearfott et al. 1993). In zoology, focus has been on, for example, sexual dimorphism in gorillas (Breuer et al. 2007), body mass in elephant seals (Bell et al. 1997; de Bruyn et al. 2009), body length of dolphins (Bräger and Chong 1999) and whales (Mocklin et al. 2010) and fin size in dolphins (Keith et al. 2001; Rowe and Dawson 2008; Rowe et al. 2010). However, apart from a recent pilot project (Wesbuer 2011, www.photomodeler.com) using Photomodeler Scanner® (PMSc®) (EOS systems Inc, Vancouver), little has been done on animal skull delineation through photogrammetry. Wesbuer's (2011) work only focused on the production of 3D models of a single *Canis familiaris* and did not record skull metrics. Several craniometric studies on marine mammals, such as fur seals, used calipers for recording linear measurements. Few successful

attempts exist using the latest technology on other morphological features such as body mass (Waite et al. 2007; de Bruyn et al. 2009). A breakthrough in craniometrics, in that researchers can now easily produce anatomically detailed, 3-D models of skulls (Wroe et al. 2005; Ross 2005; Wroe et al. 2007), allows investigating the skull morphology of two closely related fur seal species, the Antarctic fur seal (*A. gazella*) and Subantarctic fur seal (*A. tropicalis*), here using the new methodology.

Study Sites

Prince Edward Islands (PEIs)

The Subantarctic PEIs are volcanic in origin (McDougal 1971). PEIs comprises of the large (296 km^2) Marion Island (46° 54' S, 37° 45' E) and smaller Prince Edward Island (46° 13' 80 S, 37° 15' 70E), which are 21 km apart (Ansorge and Lutjeharms 2003a).

Marion Island is situated directly in the path of the Antarctic Circumpolar Current (ACC) (Deacon 1983; Ansorge and Lutjeharms 2000). It is also circumscribed by the Subantarctic Front (SAF) to the north and by the Antarctic Polar Front (APF) to the south (Deacon 1983; Ansorge and Lutjeharms 2000). Sub-Antarctic islands are classified as isolated, hostile, biologically impoverished, in which the terrestrial and marine ecosystems are relatively simple and extremely sensitive to perturbations (Ansorge et al. 2009). PEIs are surrounded by vast tracks of ocean, thus making the ocean environment a necessity for the islands' ecosystem (Ansorge and Lutjeharms 2003). Marion Island provides ideal nesting and rearing grounds for numerous populations of top predators (Condy 1981; Perissinotto and Mcquaid 1992; Ansorge et al. 2009), and supports a diversity of organisms, including breeding populations of Subantarctic fur seal *A. tropicalis* which breeds in sympatry with the Antarctic fur seal *A. gazella* (Hunter and Brooke 1992; Cooper and Ryan 1994; Guinet et al. 1996; Ryan and Bester 2008). Perissinotto and Duncombe Rae (1990); Pakhomov (1995); Pakhomov and Froneman (2000) showed that the overall productivity of this island is prone to dramatic effects due to frontal systems. Animals inhabiting these islands are exposed to varying environmental conditions during their early life stages, which could affect the development of their skeletal systems.

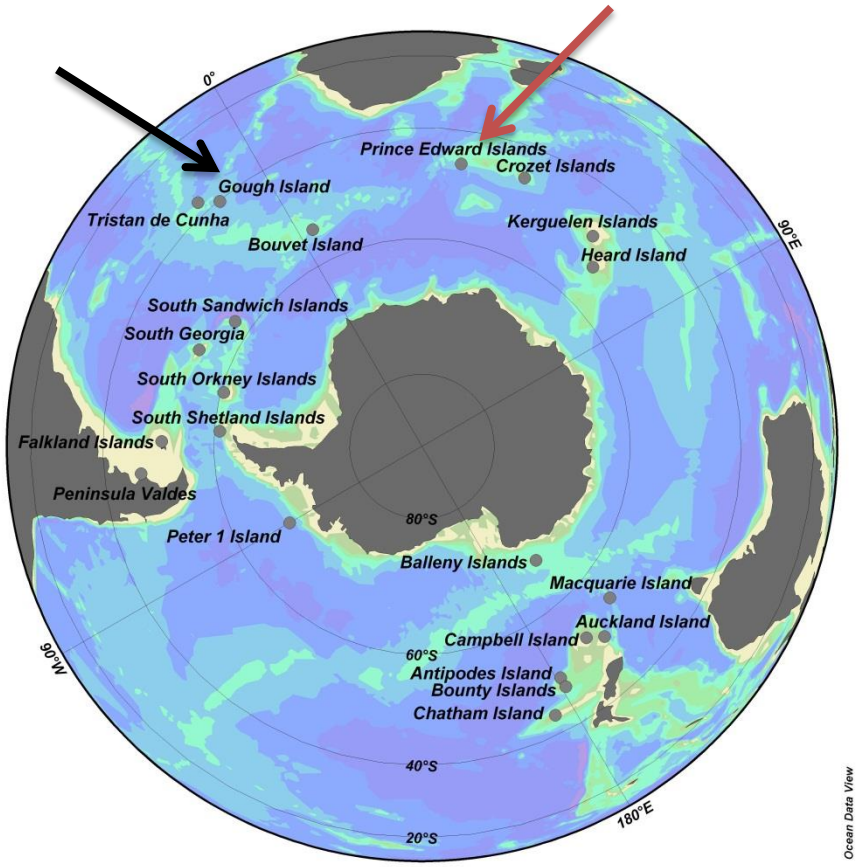

Fig.1.1 The positions of the Prince Edward Islands and Gough Island in relation to islands mentioned in the text and the continents abutting the Southern Ocean (adapted from McMahon et al. (2005).

Gough Island

Gough Island (40°21′S, 9°53′W), in the central South Atlantic Ocean, is located at approximately 3000 km from both South Africa and South America and ~350 km southeast of Tristan da Cunha (Cooper and Ryan 1994). Gough, an uninhabited volcanic mountainous island, is 91 km² in size (Wace and Holdgate 1976). The temperate Gough Island lies well north of the Antarctic Polar Front in the cool temperate zone of the South Atlantic Ocean (Höflich 1984).

Miller and Tromp (1982) classified the waters around the island as sub-Antarctic with westerly winds predominating at the island (Höflich O 1984). It is situated to the east of the mid-Atlantic Ridge and probably over a distinct mantle plume or 'hot spot' (Holdgate 2006). The high level of productivity of these waters supports numerous animals including top predators like Subantarctic fur seals. Individual organisms inhabiting these islands are subjected to varying environmental factors, such as climate, nutrient cycling, perennial systems and general geology. These affect the individuals in a distinctive way and the extent of geographic variation in body size of a given species closely parallels geographic differences in environmental variables (Meiri and Dayan 2003; Meiri and Thomas 2007).

Study Species

Arctocephalus tropicalis (Gray 1872), the Subantarctic fur seal, has a wide distribution throughout the southern hemisphere (Goldsworthy and Shaughnessy 1989; Georges et al. 2000). It breeds on temperate islands in the south Atlantic and Indian Oceans (Guinet et al. 1994). The largest populations in the Southern Ocean are found at Amsterdam and Gough islands (Bester 1987; Bester 1990; Bester et al. 2006), and the Prince Edward Islands (Marion Island and Prince Edward Island) (Hofmeyr et al. 2006). At Marion Island and Prince Edward Island they produce pups at a rate of 50,000 (Hofmeyr et al. 2006) and 30,000 (Bester *et al.* 2003) per annum, respectively and breed in sympatry with the Antarctic fur seal *A. gazella* (Peters, 1875), at the PEIs, Îles Crozet and Macquarie Island (Condy 1978).

Wilson et al. (2006) and Bester & Reisinger (2009) recorded Antarctic fur seals *A. gazella* hauled out at Gough Island as vagrants, but at Marion Island they breed in sympatry with *A. tropicalis* (Condy 1978; Kerley and Robinson 1987). Hofmeyr et al. (1997) indicated that the two species continue to hybridize to some extent. Wynen et al. (2000) and Wilson et al. (2006) both suggested that the recurrence of *A. gazella* both at Gough Island (Wilson et al. 2006; Bester and Reisinger 2009) and at Marion Island, where they hybridize with *A. tropicalis,* may result in a more compromised genetic pool of *A. tropicalis.* The population of *A. tropicalis* is, however, very large and levels of hybridization appear to be low (Hofmeyr et al. 1997; Hofmeyr et al.

2006). It is therefore unlikely that such a population could have a compromised genetic pool.

Aims and Structure of Dissertation

Aim and Objectives

This study investigates the findings of Kerley et al. (2000) and Bester and Van Jaarsveld (1994) using new methodology. There is an apparent graded latitudinal difference in adult body size of Subantarctic fur seals *A. tropicalis* (Bester and Van Jaarsveld 1994) but the skull morphometrics of adult males from two different populations were similar (Kerley et al. 2000). We aim to investigate these earlier findings on Subantarctic fur seals at Gough Island (46°54'S, 37°45'E) and Marion Island (40°29'S, 09°54'E) using a different effective approach, photogrammetry on an expanded collection of skulls. We therefore investigate whether there exists significant variation in skull properties of adult males between different populations of the Subantarctic fur seal, and as a corollary, whether Bergmann's Rule can be supported for the Subantarctic fur seal. Once an accurate, high resolution three-dimensional model of the skulls can successfully be produced, this would mean that a complete 3D skull can be digitized once and then used by any number of researchers anywhere in the world, without requiring access to the actual specimen in hand. This would reduce or eliminate the biases involved in calliper interpretation and use between different researchers.

Specific objectives are:

- To examine the usefulness of photogrammetry in seal craniometrics by comparing skull dimensions between males of two different species of fur seal (*A. tropicalis* and *A. gazella*) that can be distinguished using traditional methods (Kerley and Robinson 1987).
- To examine the usefulness of photogrammetry in seal craniometrics by comparing skull dimensions between adult males of two populations of the same species of fur seal (*A. tropicalis*) that hitherto could not be separated using traditional methods (Kerley et al. 2000).

In **Chapter two**, I embark on a test to produce an accurate, high resolution three-dimensional model of the skulls, by comparing their traditional measurement techniques with the modern technique, 3D photogrammetry.

The following key questions are addressed:

a) Can Photomodeler Scanner® produce high resolution 3D-skull models that are quantitatively accurate as compared to traditional methods?

In **Chapter three**, I investigate whether Photomodeler Scanner® could detect quantitative variations between the skulls of adult male *A. tropicalis* and *A. gazella*. I then assess which characteristics of skulls those are significantly different between the two species given that the two species are separable using the traditional caliper method.

The following questions are addressed:

a) Could Photomodeler Scanner® be used to detect the variation closely between related adult Antarctic and Subantarctic fur seal males that occur in sympatry at Marion Island?
b) Which skull properties show differentiation between the two species (*A. tropicalis* and *A. gazella*) at this locality?

In **Chapter four**, I investigate whether photogrammetric analysis reveals statistically significant differences in adult male skull properties from two different populations of adult male Subantarctic fur seals. I describe the relevance of Bergman's rule for the two different populations of *Arctocephalus tropicalis* at islands that are separated by 6 degrees of latitude and 28 degrees of longitude (Kerley *et al.* 2000).

The following questions are addressed:

a) Does photogrammetric analysis reveal differences in skull properties of adult male Subantarctic fur seals from Gough and Marion islands?
b) Which skull properties, if any, show differentiation between the two populations of Subantarctic fur seal?
c) Does *Arctocephalus tropicalis* conform to Bergmann's Rule?

Lastly in **Chapter five**, I give a general summary of the research and identify potential future research areas within this field of study.

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CHAPTER 2

Assessing 3-D photogrammetry techniques in craniometrics

Abstract

Morphometrics (the measurement of morphological features) has been revolutionized by the creation of new techniques to study how organismal shape co-varies with several factors such as ecophenotypy, heterochrony, morphological biogeography and eco-morphology. None of the techniques hitherto utilized could explicitly address organismal shape in a complete biological form, i.e. three-dimensionally. This study investigates the use of Photomodeler Scanner® (PMSc®) three-dimensional (3-D) modelling software to produce accurate and high resolution 3D models of Subantarctic fur seal, *Arctocephalus tropicalis*, and Antarctic fur seal, *Arctocephalus gazella* skulls which could allow for 3D measurements. Using this method sixteen accurate 3D skull models were produced and five metrics determined. The 3D linear measurements were compared to measurements taken manually with a digital caliper, and repetitive measurements were recorded by different people to determine repeatability. To allow for comparison straight line measurements were taken with the software, assuming that close accord with all manually measured features would illustrate the model's accurate replication of reality. Measurements were not significantly different demonstrating that realistic 3D skull models can be successfully produced to provide a consistent basis for craniometrics, with the additional benefit of allowing non-linear measurements if required.

Introduction

Marine environments are complex, dynamic and therefore in a continuous state of change. Unlike some terrestrial environments, marine systems are not always easy to study due to inaccessibility of both the ocean and the organisms that inhabit it. The need to understand changes in species abundance (whether natural or man induced) is acutely recognised (Croxall and Prince 1979) and long term studies can reveal important information about changes in these environments. Specimens are historically archived in natural history museums, where recent studies emphasized the adaptive and evolutionary significance of skull morphology divergence (Lu 2003). The comparison of the skull growth patterns between animals that were subjected to different selection pressures as juveniles, can be helpful (Lu 2003). Since postnatal skull ontogeny is subjected to several environmental factors (Calder 1984; Wigginton and Dobson 1999), this aids in understanding not only geographical variations in population's phenotype, but also their life history strategies and evolutionary changes (Lu 2003). Skulls were found to be the best material to use for morphometrics as craniometric data is consistent with genetic data in, for example lions (Mazák 2010), hence a reliable measure.

Age determination of specimens is crucial to eliminate age-related biases in the comparison of the craniometrics of animals from the same/different populations. Several age determination methods can be used to determine age in wild animals, for example through longitudinal mark-recapture, sectioning of teeth to count Growth Layer Groups (GLGs) in dentine and/or cementum of teeth, or through Suture Indexing (SI). Sutures are growth sites where the cranial and facial bones meet (Opperman 2000) and such sutures can provide insights into aging, growth, adaptations and significance of evolutionary changes of the skull (Ross 2005). The Suture Index (SI) was developed by Doutt (1942), modified by Sivertsen (1954), and suture indexing has been widely applied (Hamilton 1934; Doutt 1942; Rand 1956; Brunner 1998a; Brunner 1998b; Brunner 2002; Brunner et al. 2002). In a review of the current taxonomy of the family Otariidae, this age determination technique (SI) was successfully applied on skulls for males and females of each species of otariid (Brunner 1998b; Brunner 2002; Brunner 2004; Stewardson et al. 2008). Sutures can be used as an indicator of age (Kerley and Robinson 1987; Brunner et al. 2002;

Stewardson et al. 2008) as there exists a fair correlation between age and suture fusion (Brunner 2002). Although this renders SI a reliable method for broad age determination it is limited by species differences (Scheffer and Wilke 1953). At physiological maturity the Condylobasal Length (CBL) ceases to increase and the SI = 24 indicates the physical maturity for fur seals (Brunner et al. 2002; Brunner 2002). Therefore CBL is a very good indicator of size distinction between seal species (Brunner et al. 2002; Stewardson et al. 2008). The mechanical characteristics of the suture is subjected to multiple biological factors and suture fusion are species specific (Braga 1998), because different species have different factors affecting them (Cohen 2002). Therefore not all animals reach maximum sutural fusion in their life span (Wang et al. 2006) perhaps due to early death or predation. However, some sutures remain open throughout the individual's life time (Oelschlager and Oelschlager 2002) while some are completely closed at sexual maturity (Odontocetes: Brunner 1998a).

Craniometric measurements represent an effective tool for studying the difference in morphology of mammal populations (Gauthier et al. 2003). Craniometry has been widely used in a number of species in canids and phocids (Wyss 1994), odontocetes (Perrin 1975) and otarriids (Brunner 1998; Kerley and Robinson 1987; Kerley 2000; Tedman 2003). Previously, traditional craniometrics were conducted with the aid of calipers (Kerley and Robinson 1987; Brunner 1998b; Kerley et al. 2000; Brunner et al. 2002; Daneri et al. 2005; Stewardson et al. 2008). Through developments the standard calipers were substituted by more reliable digital calipers and were used in several recent studies (Brunner et al 2002; Stewardson et al. 2008). Although the digital caliper reduces bias as compared to actual reading on the standard calipers, the methods in which actual measurements are recorded are the same and still prone to several human errors without actual accurate repeatability (Gauthier et al. 2003). New morphometric methodological approaches are effective in capturing reliable information about the shape of an organism and result in powerful statistical procedures for testing differences in shape (Rohlf and Marcus 1993). There is increasing evidence that the improvements of 3D reconstruction methodologies will aid in 3D morphometrics studies (Zollikofer and Ponce de León 2002; Claude et al. 2003; Sholts et al. 2010; Chiari and Claude 2011; McLean et al. 2012; Ifflaender et al. 2013). The actual biological materials (specimens) are not linear as used to be

visualized in traditional methods, and the modern techniques such as 3D modelling could be more effective in enabling a researcher to visualize differences in shape (Rohlf and Marcus 1993). The size, shape and length comparison of the organism are best captured in 3D configuration of homologous land marks.

The suite of techniques currently used to measure the skull morphology includes the use of calipers (Kerley and Robinson 1987; Brunner 1998a; Brunner 1998b; Kerley et al. 2000; Brunner 2002). This means 2D or linear representation of the specimens. Despite historical and present achievement through this method, this technique has several limitations. This limitation includes the need of physical handling of specimens. Physical measurements may cause damage to the skulls, such that some features may not be measured again (Gauthier et al. 2003). A user difference in caliper readings causes poor repeatability of the actual recordings.

One of the most active fields of research in morphometrics focuses on the representation of biological specimens in a 3D configuration, and the development of approaches towards digitizing and modelling of these specimens into 3D replicas (Rohlf and Bookstein 1990). Size and 2D configuration were found to be limiting the reliability and effectiveness of the then digitizing tools. These tools worked well with larger objects and could only transform a 3D biological object into a 2D form (Becerra et al. 1993; Marcus et al. 1993).The common practice of calliper 2D measurement of objects implies that the 3rd dimension has no special biological meaning (Zelditch et al. 2004). Such reduction may lead to loss of some relevant and critical information leading to compromised and unreliable results for studies such as population variation analysis (Fadda et al. 1997).

The classical approach to morphometrics was further enhanced by the recent advent in digital methodology of 3D reconstruction that used several types of equipment including: MetraSCAN 3D, MAXscan 3D, touch probe digitizers, optical scanners, computerized axial tomographic imaging, and VIUscan. Even though these tools show relative levels of measuring success, there remain two root causes for potential errors which compromise their accuracy. Firstly, intrinsic error (i.e., the error in reading the laser line or fringe pattern), secondly, errors coming from the positioning device (Claude et al. 2003; van der Niet et al. 2010). Most importantly these techniques are either very costly or require sophisticated instruments rendering them

inapplicable in the field (Spencer and Spencer 1995; Fadda et al. 1997; Stevens 1997). A better and more comprehensive craniometrics tool is 3D photogrammetry - recording of measurements from 3D specimens' replicas using computer software.

In this study we present a photogrammetry based morphometric method using Photomodeler Scanner® software (PMSc®) (EOS Systems, Vancouver) to produce accurate, high resolution 3D biological model replicas of the skulls which allows measurements of the actual biological land marks without reduction or loss of some valuable biological patterns. Based on (1) the density of measurement (from point probing to high-density 3-D scanning), (2) portability and ease of use, and (3) accuracy, Photomodeler scanner is an accurate method for 3D modelling and measurement recording (Walford 2008). No decision on which variables should be measured is required in advance and therefore one can evaluate the usefulness of alternative suites of variables without handling the original specimens again (Rohlf and Marcus 1993).

The technique of 3-D photogrammetry by PMSc® in morphometrics was successfully used on tortoise carapace (Chiari and Claude 2011) and on horse hoof deformation (Jordan et al. 2001). In the present study I investigate whether photogrammetric analyses will provide the required accurate and high resolution, three dimensional (3D) models of Subantarctic fur seal skulls, to determine whether there exists significant differences in skull properties of adult male Subantarctic fur seals from two spatially separated populations. We used randomly collected skulls to measure the selected metrics. The variables were recorded by both the digital caliper and through the PMSc® 3D models by different users, and then compared to test whether photogrammetric analysis reveals statistically significant differences in the same metrics measured by different methods.

The hypothesis is that where $p < 0.05$, the methods produce different results of the same variables

Materials and Methods

Study area

The samples used in this study come from Marion Island (MI) (46° 54' S, 37° 45' E) and Gough Island (GI) (40° 29' S, 09° 54' E) which are separated by 3,800 km and 6^{o} latitude, 26° longitude.

Specimens

Skulls of eight *A. tropicalis* and eight of *A. gazella* (Table 1a) were modelled into high resolution 3D replicas. The species difference is not of importance in the context of this chapter.

Camera hardware

This technique does not require any specialized cameras other than those with high resolution (high megapixels) that gives high levels of accuracy. A calibrated (see below) Kodak Easy share C 195 camera (A) 14 megapixels and a Sony DSC-W70 camera (B) with 7.2 megapixels was used in this study.

Software

The computer software programme PMSc® was used to create a dense 3D points cloud and detailed surface models of skulls of the two fur seal species. The photograph-based scanning software then compares two photograph based patches of smart points

Procedure

Each specimen was given a number and was identified by the Port Elizabeth Museum catalogue. The setup (table legs and table surface) where the photogrammetric accessories (Lazy Susan rotating wheel & traffic cone onto which each skull was perched for taking pictures) were demarcated with measuring tapes and permanent markers, and left unmoved throughout the photographic sampling procedure to eliminate any shifting from where they were fastened to the floor (Fig 2.1). Reference points were marked on each skull with an ink pen (*see setup section below*). To ensure high accuracy and reliability of reference points some natural skull features which were to be measured were also marked. The condylobasal length (CL) and the skull height (SH, at the level of the bullae) were determined manually

by vernier calliper and digital calliper and used as additional reference points. Five metrics were recorded for comparison of the two methods (Fig 2.3)

The Ringed Automatically Detected (RAD) Coded Targets were printed on sticky paper and pasted throughout the surface area of the cone avoiding reflections and bubbling which may affect the distinctness of the coded targets. The software can recognise each coded target individually which aids in automating and standardizing identification of the points and subsequent orientation of photographs, thus avoiding the bias of manual marking of points. Preliminary photographs were taken to test the angles, distances, and quality of the setup. The detectable irregularities in the experimentation setup were corrected before actual photography. The photograph orientation quality was maintained at 40+ coded targets per photograph (Fig 2.2 and Fig 2.4).

Calibration

Before introducing the cameras into the experimental setup (Fig 2.2), the cameras were calibrated for close-range photogrammetry (Fig 2.1). The camera was switched to “program mode shooting” to stabilise internal parameters, to make sure all parameters remain constant throughout the experimentation, including zoom settings to maintain constant focal distance. Added features such as red eye reductions were switched off to reduce noise in calculations. The calibration grid with four corner Ringed Automatically Detected (RAD) Coded Targets (Fig 2.1) was printed on an A4 page to suit the project size and type for close-range photogrammetry. This provides accurate calibration of the entire field of view and determines the principal point (at the intersection of photographs and the optical axis of the lens) and compensates for orthogonal distortion and conversion (Remondino and Fraser 2006; de Bruyn et al. 2009).The camera was fully calibrated by taking photos of a grid pattern that is familiar to the software and running these photographs through the camera calibration wizard (see Photomodeler Scanner® help files for details). The calibration grid is included as part of the software package. The A4 calibration grid or coded target sheets was fixed to a uniformly dark floor to avoid movement during calibration. The uniform background helps the software to avoid identification of marks that are not part of the calibration grid. Eight to twelve photos were used for optimal calibration to achieve maximum photograph coverage and accuracy. A good point coverage and photograph coverage was attained at 91% coverage view. The

maximum average 'residual error (RMS)' of each project was maintained below 1.5, as recommended by the software (see Photomodeler scanner® help files). The validity of the high level of accuracy in 3D production (Deng and Falg 2001) and of accuracy in point-based 3D volumetric measurement systems (Graff and Gharib 2008) is acceptable. Once the calibration was completed successfully the calibration project was saved for future use. The complete characteristics of the camera such as the focal length, imaging scale, image centre, principal point, the digitizing scale, and format aspect and lens distortion were fully saved in the PMSc® software library. Photographs from cameras that have been previously calibrated could then be loaded into the programme and immediately linked to the calibration data associated with that camera/lens.

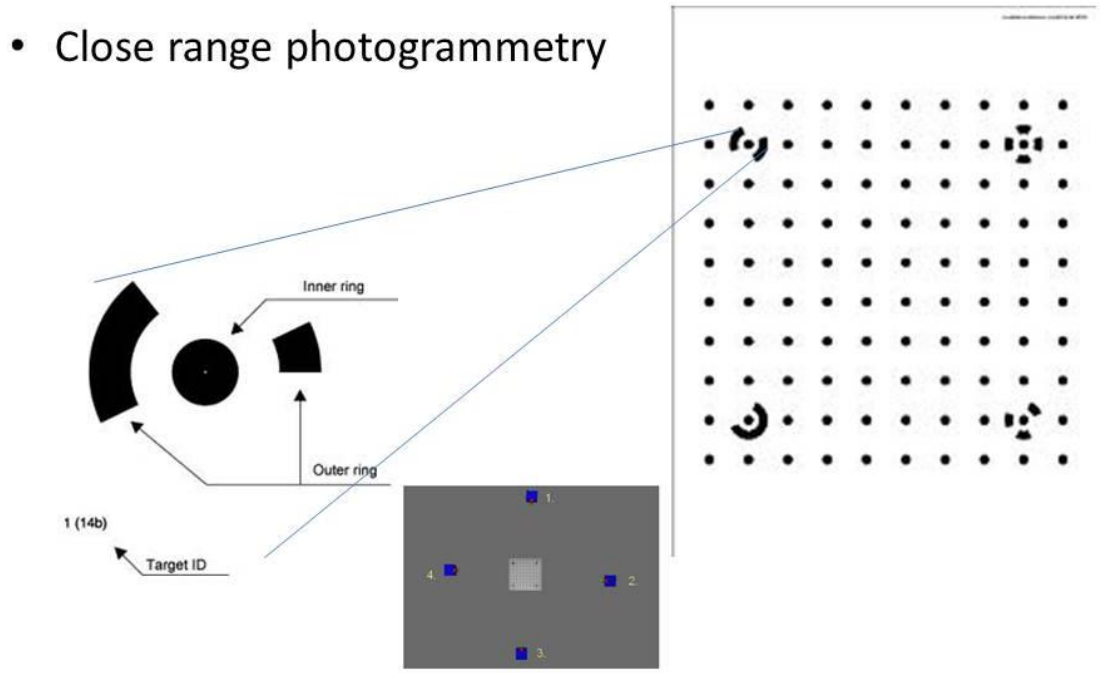

Fig. 2.1. Calibration sheet, used to calibrate the cameras used in the study (see more details in the Photomodeler® help files).

Photo-based scanning is first based on a strong photogrammetric core. That means the system is capable of calibrating cameras, and is able to accurately solve for the position and orientation of the camera when the photographs are taken.

Camera Setup (Coded Target)

During photography, two cameras were mounted on tripods and stationed at approximately 1.5 meters and 0.7 meters above the floor pointing to the subject, approximately 35 cm apart from each other. Once the cameras were mounted on the tripods, the tripods' leg positions were marked on the floor and affixed in position so as to avoid shifting of the assemblage. Camera A (higher resolution, 14 mega pixels) was tilted down at 30 degrees and Camera B (lower resolution, 7.2 mega pixels) was tilted up at 10 degrees from horizontal so that all surfaces of each skull in any particular vertical plane could be covered, from the condyles to gnathion. The distance between the skull and camera B was 55 cm and skull to camera A was 75 cm. The standard ceiling light was augmented by extra light source mounted on a stand, behind the cameras but at such a height and downward angle so as to illuminate the skull, without casting camera shadows onto the objects, avoiding background reflections at the same time. The background behind the skulls and lazy Suzan was uniform black to avoid automatic identification of the backgrounds points.

Twenty four photos were taken per camera for each skull, encompassing the entire skull area. To facilitate this, each skull was mounted on a 28 cm high plastic traffic cone with a 15 x 15 cm square base area tapering to a round opening 4 cm in diameter. The skulls were oriented vertically with the tip of the cone fitting snugly in the *foramen magnum*. The cone was mounted on the absolute centre of a 270 cm diameter glass Lazy Suzan (LS). The wheel surface was covered in matt black paper to avoid reflections and the LS base taped in a fixed position on the table surface. The entire surface area of the cone was covered with coded targets, distinguishable by their inner ring diameter. Ten strips of corded target were affixed on the lazy Suzan (Figure 2.2). Using marked out angles radiating from the centre of the wheel, each skull was advanced through 15 degrees from a fixed starting point before a photograph was taken of the skull in that plane by each camera from their fixed positions. Once the skull had been rotated through the 24 positions (i.e. 360 degrees), 48 digital images of the particular skull were now available for further processing.

The software identifies unique RAD coded targets to orientate the cone and skull set-up with reference to each camera position, in three-dimensional space. The photographs are thereby automatically orientated. One can manually identify the points on the skull (that were marked with an ink pen) for the software to aid in further orientation of the surface plane of the object to be modelled (see below).

The software then uses the Smartmatch® functionality to automatically cross-reference points in a selected area (in this case the skull) and the coded points to create an accurate 3-D space. It is also a requirement that the Root Mean Squared (RMS) error should be maintained at <1.00 residual, meaning that the models will be accurate (Deng and Falg 2001). The area within each photograph occupied by the skull is delineated and a dense point cloud mesh is created as a projection of the skull. The density of points that the software concentrates into this dense point cloud dictates at what pixel resolution the skull can be modelled, and is thus related to the resolution of the camera/lens. This serves as a key step in the later identification of skull landmarks for measurement.

Linear measurements

Random skull linear measurements were recorded by both vernier and digital calipers to the nearest 0.01 mm and used as reference and comparison values on the skulls. The recorded values were used as reference values to the scale that is manually defined by the user. Some traditional linear measurements were also recorded using the callipers and this was used to evaluate the precision of the measurements done through the software.

Imaging and processing

For the purposes of the study, two methods (tools) of 3D modelling were used which are both available in the Photomodeler scanner® software package. The two methods used vary in how the images are taken, and with the algorithm processing during the initial stages. Both methods use a pair of geometric points to produce a dense point cloud model. The Coded Target and Smartmatch® methods use the Coded Target points and the smart points respectively. One calibration can be used for both modelling methods. The detailed processing step by step for both coded

target and smart match methods can be found in more detail in the software tutorials and help files. The Dense Surface Model (DSM) area of interest was defined by using the DSM Trim tool. The dense surface tool was used to perform the DSM in pairs of best photographs, based on predetermined values which could later be changed to modify the 3D model.

Photomodelling method (tools)

The first tool that was considered for this study is the automatic coded target method. The coded target method uses RAD targets, for accurate sub-pixel point marking. This automatic recognition allows for automated referencing even before a project is processed, the point's ID is coded in its ring, and thus the point can be identified in each photograph that it is marked in and therefore can be referenced automatically. The points to be targeted were placed on the entire surface area of the cone arranged in the 360 degrees pattern for the 3D model. The size of the scene was determined and the maximum distance between a camera and a target was calculated to aid in coded target size recognition. Using the Automatic Target Marking the photographs were automatically detected by RAD. The sub-pixel and the coded targets were referenced in each image with more than 40 targets in four photographs through a series of steps the fully referenced high resolution 3D skull model was produced.

Fig. 2.2 Image acquisition and camera setup for coded target photography of museum skulls.

The second tool that was used is the fully automated Smartmatch® method which automatically marks and references points on natural features and generates 'Smart Points' then orients and processes the photos to provide fully automatic project set up and orientation for non-targeted projects. The special capability of Smart Match that differs from coded targets is that it searches out natural feature points in images, matches them between photos, and generates 3D *x, y, z* points automatically, Smart Match can be differentiated from the coded target tool in that it does not require inserted targets, but rather it requires an object to have appropriate texture so that intricate features in each photograph can be matched between photos. The skulls that were too bright/white were dusted with chalk dust before photography to enhance the texture.

A maximum of 18-20 photographs were taken at a distance of ~45 cm from the skull. The photos were taken at an overlap of three photos and low angles (~<30) between photos, to maximize the cross matching between photographs. The photography studio was designed to avoid reflectivity and glare (see above). The photography for each Smart Match project was done inside a room with constant lighting to

minimizing effects of lighting changes in Smartmatch® capabilities. The photographs were all taken in Program mode without flash with camera parameters kept constant. The side lighting and shadows were also minimized by covering windows and other mediums of reflection with a black cover. The camera was fixed with a tripod at a moment of shooting each photograph throughout the project to maximize the focus of the photographs taken. The background was designed to be constant at all points of shooting. The ordered surround Smart Match system of photography was selected for the 360 degrees sampling of each skull.

Upon completion of the photography the photos were uploaded into the PMSc® software, and an option of Smart Match was selected as opposed to the Coded Target in the project wizard menu. The calibration setting was recalled from the PMSc® camera library. The project was run for automatic referencing, matching and marking through the software matching algorithm. A very low (<45 degrees) angle was maintained between photographs. Each project was maintained within the prescribed residual error (RMS) of 5.0, for accurate projects (see Photomodeler Scanner® help files for details). The photos were matched and orientated. The scale was determined from pre-marked points during photography, and referenced in all photographs for 3D using the PMSc® scale wizard. The project was processed for dense surface models (DSM) similar to the DSM in the coded target project to process the project for final 3D modelling. The measurements were recorded in the point mesh edit mode.

Statistical Analysis

The recorded measurements through digital caliper and PMSc® from the 3D skull models were tested for normality using the Shapiro-Wilk normality test. Then the data was tested to determine the similarity/differences using an F test from all normally distributed data. All normally distributed data were further tested using the Welch Two Sample t-test for difference determination and data that was not normally distributed were tested for significant difference using the Kruskal-Wallis rank sum t-test (Table 2.1 & 2.2).

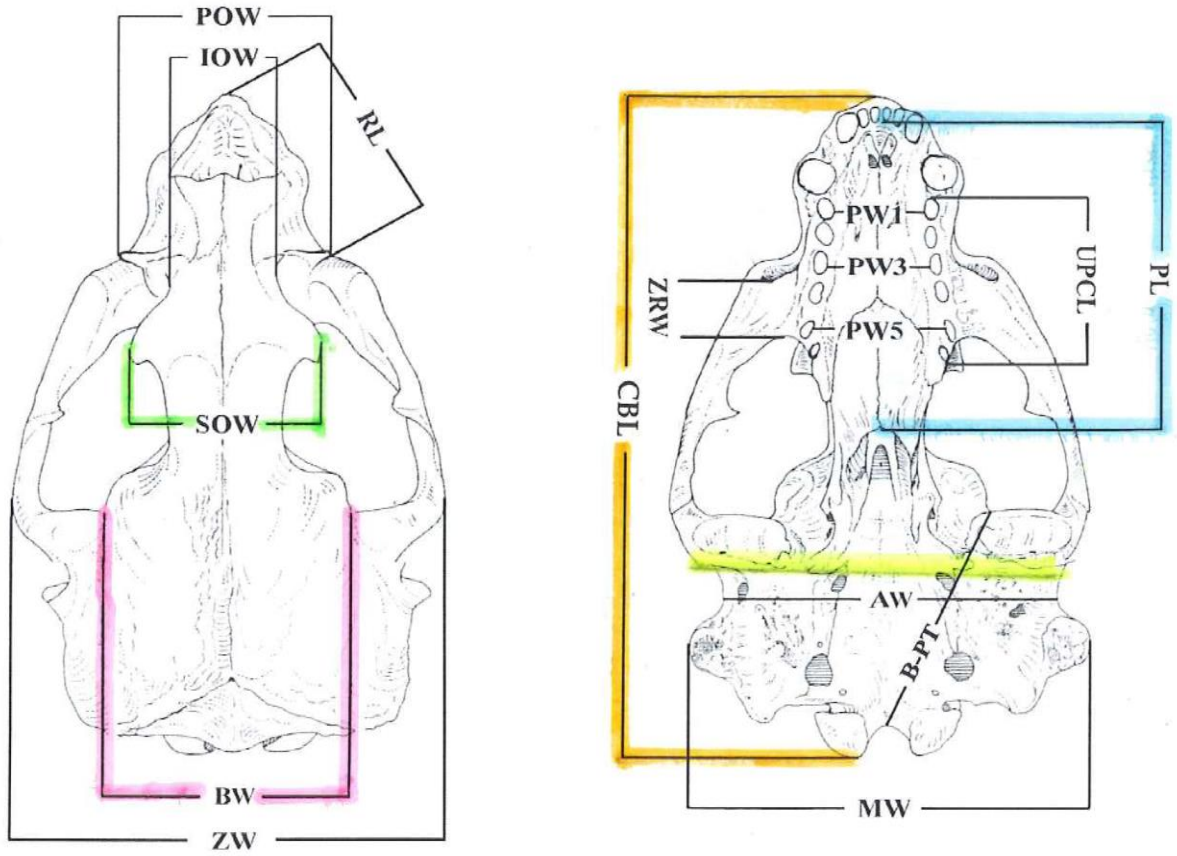

Fig 2.3. Skull measurements (highlighted) used for the purpose of this study (VW, Ventral width; BW, braincase width; CBL, Condylobasal length; PL, palatal length; SOW, supraorbital width. Figure from Daneri et al. (2005).

Results

3-D Modelling

Sixteen high resolution 3-D skull models were produced from sixteen skulls (eight for each species, *A. tropicalis,* and *A. gazella*). The species difference in this chapter was inconsequential, any species can be utilized. The two (Coded Target and Smart Match) PMSc® tools were used to produce the 3-D models. Although the models produced by the coded target were acceptable, it was not of sufficient quality to provide desired high resolutions for accurate measurements due to low megapixel coverage per photograph. Only the models produced through the automatic tool (Smart Match) were used for the recording measurements, which were further considered for variance analysis between the two methods, Photogrammetry and Traditional (Caliper), because they were of higher resolution.

Similarity analysis

A total of 16 fur seal skulls were modelled, eight per species (*A. tropicalis* and *A. gazella*). Five variable measurements were recorded from the 3-D models and compared with the same variable measurements recorded with a digital caliper (Table 2.1, Table 2.2 and Appendix A).

Table 2.1. The summary of minima, means, quartiles and standard deviation for all tested variables to compare the two methods of measurement, by calliper, and 3D PMSc®.

Variable	Min	1st Qu.	Median	Mean	3rd Qu.	Max	Standard Deviation
Condylobasal length	206.6	222.7	224.7	225.2	228.3	240.4	0.43
Supraorbital width	38.48	45.08	49.01	50.87	54.80	69.51	0.18
Braincase width	51.61	54.00	57.88	57.29	59.70	65.04	0.34
Palatal length	68.11	75.78	79.50	79.11	82.62	90.20	0.29
Ventral width	18.38	23.07	31.10	29.44	36.26	38.36	0.27

Table 2.2. The Shapiro-Wilk normality test , F test, and Kruskal-Wallis rank sum test results, for five measured variables recorded by caliper and PMSc® (*P*= Significance, F = f value for f test, t = value for t test, w = value for Shapiro test, M.x = mean for x , M.y= mean for y).

Variable	Shapiro-Wilk normality test		F test		Kruskal-Wallis rank sum test			
	p	w	F	*p*	t	*p*	M.x	M.y
Condylobasal length	0.0802	0.9411	1.0521	0.9230	-0.0255	0.9798	225.21	225.2809
Supraorbital width	0.1034	0.9449	1.0122	0.9816	-0.0142	0.9997	50.8675	50.8686
Braincase width	0.2668	0.9595	0.9884	0.9823	-0.0122	0.9903	57.282	57.298
Palatal length	0.4986	0.97	1.0312	0.9533	-0.0181	0.9856	79.093	79.130
Ventral width	0.00215	0.8814	0.9921	0.9879	N/A	0.4514	N/A	N/A

The SPSS software package 21.0 (SPSS Inc. IBM, South Africa) and R software package 2.14.2 (R development Core team 2012) was used to perform basic statistics. The test for normality showed that our data was normally distributed in four variables not the fifth, the vertical width (Table 2.2). All variables subjected to

analysis of variance (F test) between the two methods, caliper, and PMSc® (Table 2.2), showed no significant differences between the two methods. The normally distributed data for four variables (CL, SO, BC, PL) subjected to Welch Two Sample t-test, and the non-normally distributed (VW) subjected to Kruskal-Wallis rank sum test (Table 2.2), showed that the two methods produced similar results. However, in Box-plot a, for CL (Fig 2.4) PMSc® is shown to be more sensitive to the variations present. The value of *p* for all five recorded variables was very high (0.45 to 0.99) indicating that the methods produce similar results. Of the five variables used, one (supraorbital process p=0.999) showed a very strong factor of similarity, followed by the braincase width (p=0.990). The PMSc® is sensitive to minute variations as it detects more outliers, which can be identified in CL comparison.

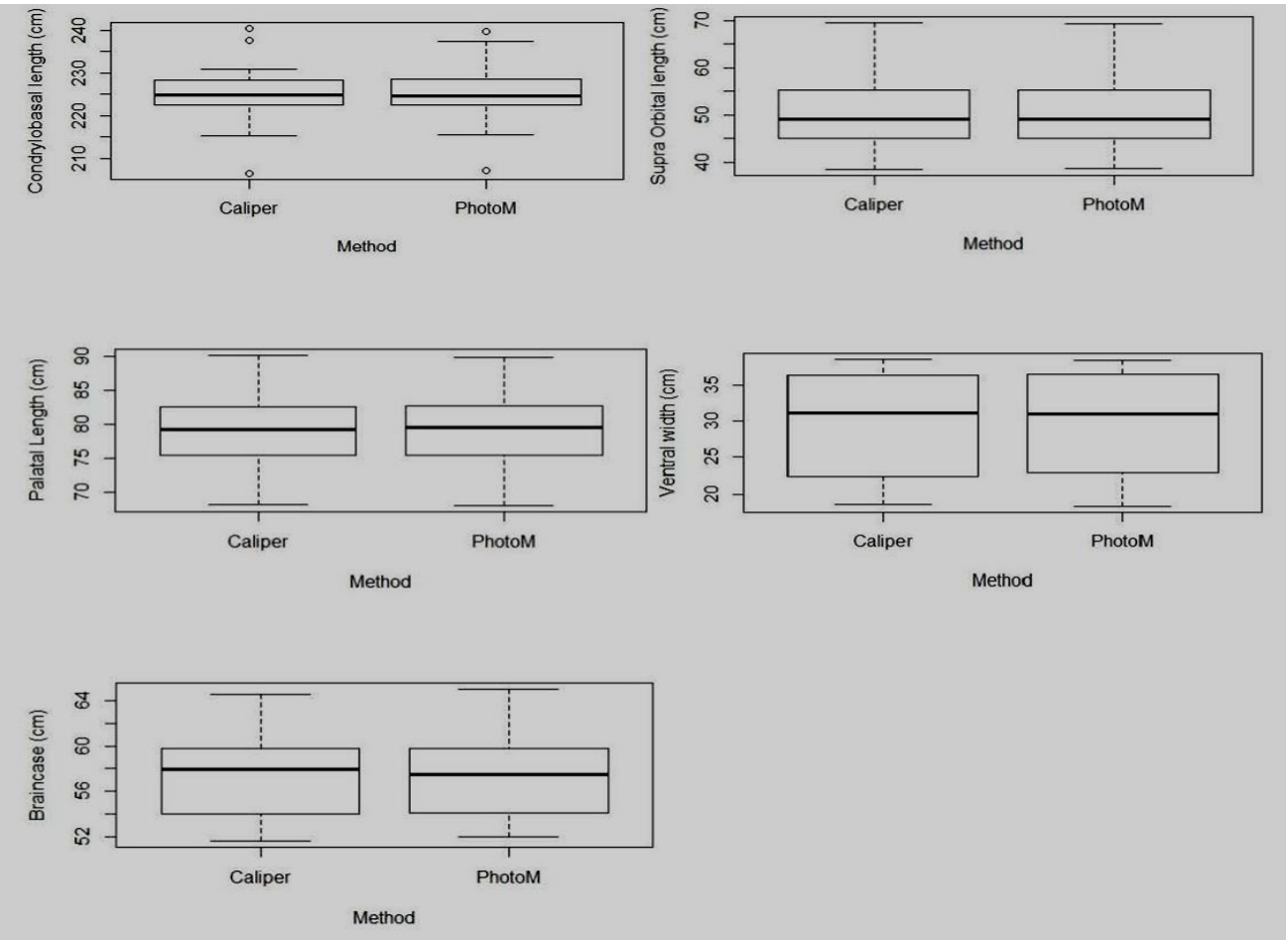

Fig 2.4. Similarity analysis (F test, Welch Two Sample t-test, Kruskal-Wallis rank sum test) between PMSc® and Caliper measurements, Median, Interquartile range, and outliers of the measured variables used for the comparison of caliper and 3D PMSc® measurements.

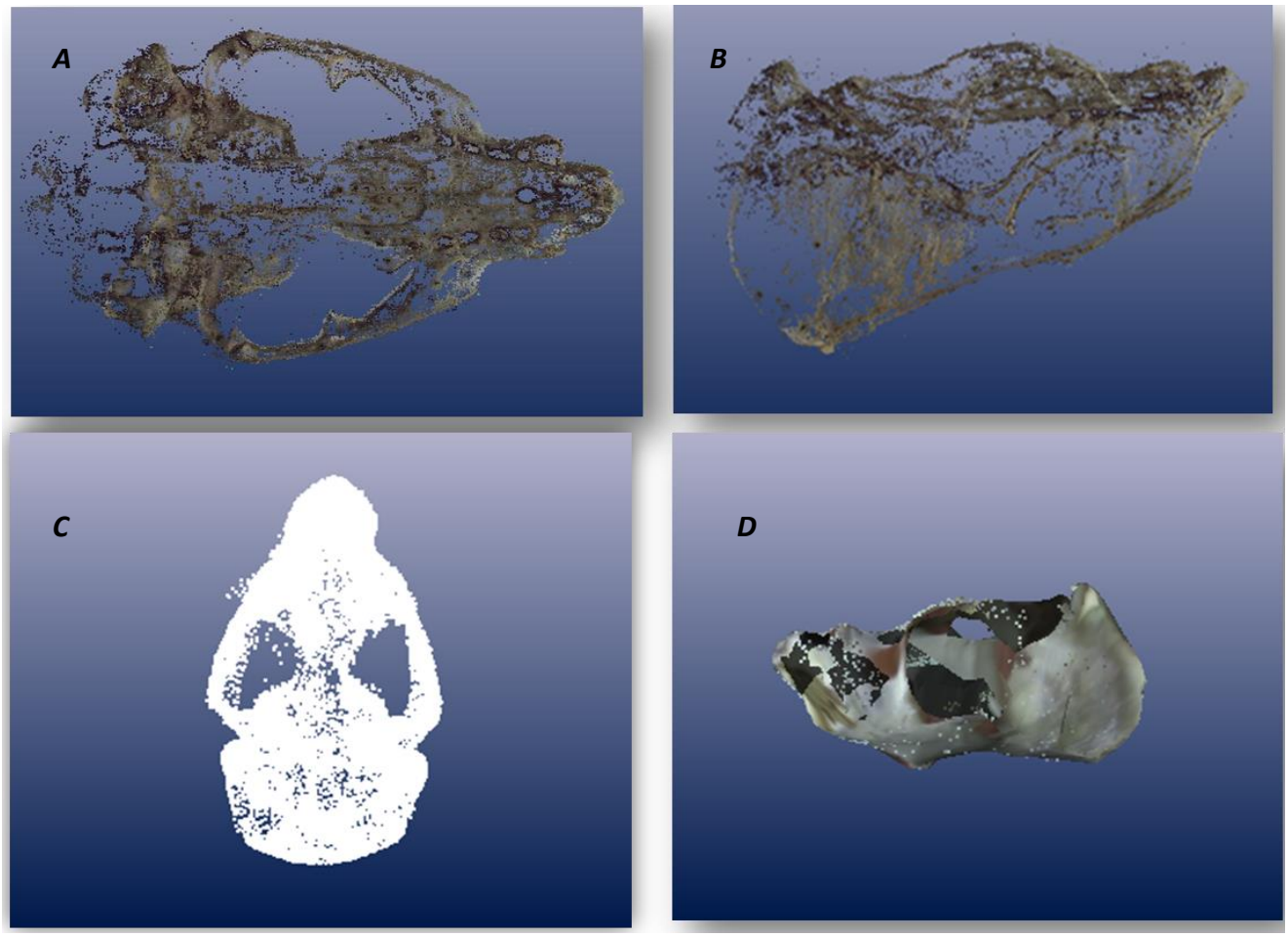

Fig 2.5. Set of 3D modelling at various stages of processing using Photomodeler Scanner®, A, Initial stage of natural skull features extraction, B, Three-dimensional modelling of the natural features, C, 3D skull in the default and dots surface layer, D, partially complete 3D model used for measurements.

Discussion

The results show acceptable recordings for both tools used for 3D modelling. Both Coded Target (CT) and Smartmatch® (SM) methods (tools) worked well in constructing the 3D skull models. Alby et al. (2009) also produced smooth 3D models with PMSc®. Both tools worked equally well at ambient light. However with CT it is necessary to initially standardize the experimental structure as an integral part of the photography and has to remain stable throughout the experimentation. The SM on the other hand only requires good lighting condition without rigorous setups and is more user-friendly as compared to the CT. Due to the required degree of constant

stability of the experimentation structure the CT project is more susceptible to unintended human errors. However, both methods do not have too many intensives needs for the operation of modelling. In terms of time required to obtain the final 3D skull model, the SM method is more effective than the CT method. The PMS models reach submillimetric precision (Jordan et al. 2001; Alby et al. 2009), as the SM picks up minute details of the natural features on the skulls and automatically performs the referencing, then arranges the images in 3D modelling format (See Fig 2.6 below). Importantly, this minute detail capture is derived by the camera/lens resolution available from the camera.

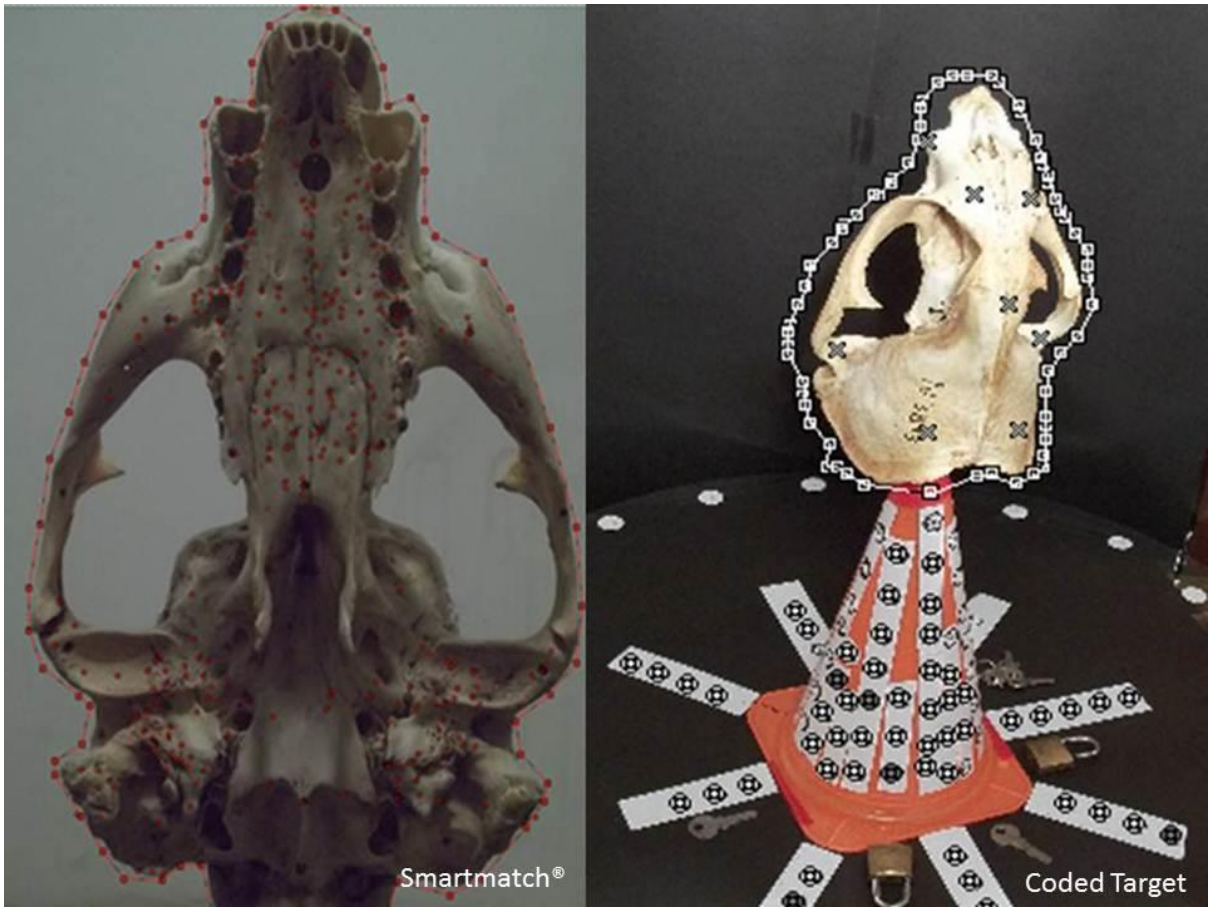

Fig 2.6. Smartmatch® and Coded Target images during fur seal skulls 3D acquisition.

Although these two tools share common stages of processing, it also differs in the degree of manual operation required to attain the final 3D model. The four main reasons that the CT was used in projects are: a) to automate 3D point measurement using Automated Coded Targets, b) to increase the speed at which projects can be

completed, and robustness of the crucial orientation stage in projects that use a mixture of coded and manually marked targets, and c) to improve robustness and reduce the chances of acquiring incorrectly referenced points. The successfully produced 3D models from the CT were of a compromised resolution that might be attributed to large distances between the skull and the cameras. The large distances between the skull and the cameras resulted in images covering a large portion of the surrounding area where the skull was placed. Only approximately 10% of the image was occupied by the skull, and the photographs had an inadequate coverage (effectively utilizing only 1.4 megapixels of the available 14 megapixels). Although the resolution obtained at 1.4 megapixels was inadequate, a reduction of the distance between the cameras and the skull would promote maximization of the photograph coverage of the skull which could improve the results. The improvements of the photograph coverage in camera calibration could also be used to improve the results. The SM tool is preferred because it automatically detects natural features in photos and reliably matches these features between photos. A photo-based scanner's accuracy and resolution are affected by the resolution of the camera used, the distance of the camera to the subject, and the nature of the texture and pattern on the skull surface. In addition, SM requires little human or manual intervention which ensures more accuracy with less human errors. It also has a multi-purpose feature in that: 1) it gives quick project setup and orientation of all photos, 2) operates at low to medium density point clouds for analysis, measurement, and surfacing, and 3) uses point clouds for approximate surface setup as a precursor to Dense Scanning. The sum of factors that maximized the software tool of choice were camera calibration, the camera setup, total number of photographs taken, lighting conditions and sampling intervals.

Comparison: PMSc® and Caliper.

The trials to evaluate the accuracy of the photogrammetric method and the traditional method (caliper) measurements are presented in Table 2.1. Measuring and calculating the skull metrics and *p*-values enabled a comprehensive evaluation of the PMSc® (Walford 2008) and traditional method (caliper-measurements) (Stewardson et al. 2008). Skull metrics can be precisely recorded by the two methods (this study) and the *p-values* indicated that PMS recordings and calliper

recordings are comparable. This study has further demonstrated the high efficiency of the PMSc® both in time and repeatability of recorded values. Therefore the PMSc® produces very good 3D skull models which are true replicas of the actual skulls. This adds to the advantage of acquiring the biological information of organisms in their biological form or 3D configuration (Rohlf and Marcus 1993), thereby reducing the risk of losing critical information (Fadda et al. 1997). Compared with the traditional method measurements, the photogrammetry method is significantly more efficient and accurate (Wang et al. 2006). The PMS technique can benefit both linear and volumetric studies (Graff and Gharib 2008) as it is more adapted to any object dimension (Alby et al. 2009).

Finally, a number of important limitations need to be considered. First, the study did not evaluate the use of shape holistically as a determinant of variation or similarity. Secondly the current research was not specifically designed to evaluate factors related to volumetric measurements and inclusivity of possible measurements. This is mainly due to shape and volume determination of skulls being a potentially damaging procedure for museum specimens. Considerably more work will need to be done to determine the use of volume measurements and reducing dependence on linear metrics.

Conclusion

PMSc® produced accurate and high resolution, three dimensional (3D) models of fur seal skulls. The same approach can be applicable to other object of interest which may be considered for 3D modelling. This method also offers a non-invasive, time effective and cost effective (once software had been purchased) way to produce an accurate high resolution 3D model of a skull and offer exceptional options of recording different types of measurements from the models, which may be developed into volumetric measurements. Of particular interest is that in using this method, an entire museum specimen collection can successfully be digitized, the digital images and 3D models of these can be accessed at any locality and used by any number of researchers without requiring the actual specimen at hand. Future research should also be directed at collective mass and volume estimation of the digitised models.

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CHAPTER 3

Comparisons of adult male fur seal (*Arctocephalus gazella* and *A. tropicalis*) skulls using photogrammetry

Abstract

The related, but separable on external characteristics and vocalizations, Antarctic and Subantarctic fur seals occur in sympatry at Marion Island. Skeletal material allowed separation through skull morphometrics in earlier studies using traditional methods. This study investigated the use of photogrammetry to compare the craniometrics of Antarctic fur seals, *Arctocephalus gazella* (n = 8), and Subantarctic fur seals, *Arctocephalus tropicalis* (n = 8). Eight skull metrics were compared between adult males of the two species. Despite historical factors, such as sealing, local adaptation, and possible genetic drift, all tested cranial measurements showed differences between the two species. Therefore, the software package Photomodeler Scanner® (PMSc®) proved to be an effective and reliable tool for craniometric separation of adult males of these fur seal species, and matches the traditional methods.

Introduction

Seals roamed freely in large numbers in the Southern Ocean radiating from several islands, until commercial sealing began in the late 18th century and through to the early 19th century (Bonner and Laws 1964; Rand 1956; Shaughnessy 1976) which had reduced their populations. The intensive seal harvesting brought the populations of fur seals to the brink of extinction (Shaughnessy 1976). The populations of Subantarctic fur seal, *A. tropicalis,* and Antarctic fur seal, *A. gazella,* also suffered severe degrees of exploitation which left this species near extermination (Bonner and Laws 1964). Sealing resulted in local extinction at some localities (Shaughnessy 1982; Roux 1987). Remnant populations were recorded at Gough, Amsterdam and Marion islands (Bester 1987; Kerley 1987; Roux 1987). Surviving individual populations of *A. tropicalis* were estimated at 500 and 300 at Gough Island and Marion Island respectively (Shaughnessy 1976) while *A. gazella* surviving at Bouvetoya and Bird Island-Willis group were ~ 1200 and 100 respectively (Bonner and Laws 1964; Fevoden and Sømme 1976). This might have had negative effects on fitness of the populations as a result of low or compromised heterozygosity (Caughley 1994), likewise the hybridisation detected at Macquarie Island between Antarctic and Subantarctic fur seals affected the seals gene pool (Wynen et al. 2000; Lancaster et al. 2006; Lancaster et al. 2007a; Lancaster et al. 2007b). Since the early 20th century no commercial sealing took place (Condy 1978). The fur seal population flourished and recolonized the islands after sealing ceased (Bester 1980; Kerley 1983a; Kerley 1983b). Approximately 90 per cent of the world's populations of Subantarctic fur seals occur at both Gough Island and Marion islands; with >200 000 and 48 000 individual seals respectively (Bester 1990a; Hofmeyr et al. 2006) and 97% of Antarctic fur seal populations occur at South Georgia (Hofmeyr et al. 2006).

Vagrants move over 1000's of kilometres from their native breeding grounds (Payne 1979; Goldsworthy and Shaughnessy 1989). Subantarctic fur seals exhibit a high ranging capability, lactating females travelling in excess of 600 km (Bester 1987; Robinson et al. 2002; de Bruyn et al. 2009) from their native islands during foraging trips. A subadult had travelled 7000 km from its breeding ground at Amsterdam Island to Gough Island (Hänel et al. 2005) . There has also been several sightings of subadult vagrants outside their native breeding grounds at a variety of locations, e.g.

South Georgia (Payne 1979), South Africa (Shaughnessy and Ross 1980), Angolan coast (Orr et al. 1970; Carr et al. 1985), the coast of Antarctica (Shaughnessy and Burton 1986); Brazil (Pinedo 1990); New Zealand (Taylor 1990); Australia (Gales et al. 1992); Comores (David and Salmon 2003); Madagascar (Garrigue 1996), Mauritius and Rodrigues (David and Salmon 2003); Bouvet Island (Hofmeyr et al. 2006); Zanzibar, Tanzania (Hofmeyr and Amir 2010), Gabon (Zanre and Bester 2011), and most recently at Livingston Island (Torres and Aguayo 1984). Bester (1981) proposed that rapid population increase, accounted for the population instability at breeding grounds, resulting in high numbers of extralimital sightings. This may suggest that there is high potential of inter-island movement between Gough and Marion islands.

Rand (1956) provisionally identified the fur seals on Marion Island as *Arctocephalus gazella* (Peters 1875). Subantarctic fur seals and Antarctic fur seals were once considered conspecific (King 1959). King (1959) suggested the existence of two subspecies of southern fur seal, *Arctocephalus tropicalis gazella,* and *Arctocephalus tropicalis tropicalis*, one occurring south of the Antarctic Convergence and one to the north of it. Repenning et al. (1971) revised the genus *Arctocephalus* and accorded specific status to King's subspecies, and recognised the species concerned as *Arctocephalus tropicalis* (Gray 1872), formerly known as the Amsterdam Island fur seal occurring north of the Antarctic Convergence and *Arctocephalus gazella* (Peters 1875) the Kerguelen fur seal, occurring to the south of the Convergence, similarly as they are still classified (Berta and Churchill 2012). Condy (1978) mentioned the unusual skull in the Rand collection which was the first indication that both species might be present on Marion Island. The related Antarctic- and Subantarctic fur seal occur in sympatry at Marion Island (Condy 1978; Hofmeyr et al. 1997) although they prefer different habitat types on the island (Hofmeyr et al. 1997), hence very low rates of hybridization have been recorded at this locality (Hofmeyr et al. 1997; Maboko 2009). No recorded inter-island movement of fur seals between Marion and Gough islands exists (Condy 1978). However, the recorded capability of dispersal of *A. tropicalis* may suggest the opposite.

Geographic variation in characteristics has been tested successfully through skull morphometrics in a number of studies on various species (Orr et al. 1970; Kerley

and Robinson 1987; Boyd 1993; Le Boulenge et al. 1996; Gao and Gaskin 1996; Borjesson and Berggren 1997; Kerley et al. 2000; Brunner 2002; Brunner et al. 2002; Freckleton et al. 2003; Endo et al. 2004; Fornel et al. 2010). The inter-population comparison of somatic features such as cranial dimensions between different species occurring at the same locality, and with some degree of cross breeding might provide more insight into the understanding of the degree and extent of hybridization.

The aim of the study is to investigate the craniometric differences/similarities between *A. tropicalis* and *A. gazella* from Marion Island where they breed in sympatry (Hofmeyr et al. 1997; Hofmeyr et al. 2006b). We seek to use the newly developed method of recording craniometric measurements through 3D photogrammetry, and to test the reliability and relevancy of photogrammetric measurements of skulls of the two different species which can be differentiated using conventional measuring techniques (e.g., Kerley and Robinson 1987).

Materials and Methods

Skulls of adult male *Arctocephalus gazella* and *Arctocephalus tropicalis* collected at the islands (over the period 1977 to 2008) were used. The skulls were de-fleshed and boiled in water until the flesh could be removed easily. Skulls were then washed with mild detergent with water and air dried at room temperature. The male Subantarctic fur seals were shot (1977 to 2008) with a 0.22 rifle from close range at breeding, non-breeding and idle colony sites (defined in Bester 1982) at Gough Island and Marion Island (Condy 1978; Kerley and Robinson 1987; Bester 1990; Kerley et al. 2000), and natural mortalities were included in the sampling as well, and cleaned as explained above.

Age determination was based upon incremental lines in the dentine of sectioned canines (Bester 1982; Bester 1990a). The confounding effects of age and sex were further removed by including only adult males over the age of eight years which was determined by the skull suture index (Sivertsen 1954) following Brunner (2002), this age lies at the inflection point of the growth curve for Condylobasal Length CBL for *A.tropicalis* as determined by Bester & van Jaarsveld (1994), and cross-referenced with the estimated ages (from tooth sections) when available (Bester 1990).

Suture index

All specimens (A. tropicalis and A. gazella skulls) were aged on the basis of suture indexing (SI) of Sivertsen (1954). Nine cranial sutures (Fig. 3.1) from skulls were assigned a value of 1 to 4, according to the degree of closure (1 = suture fully open; 2 = more than half open; 3 = suture more than half closed; 4 = suture fully closed), which translates into an index (SI), ranging from 9 (all nine sutures fully open) to 36 (all nine sutures fully closed). These values were then added together to give a total suture index (SI) for each skull, as used in Sivertsen (1954), Kerley and Robinson (1987), Brunner (1998a,b), Kerley et al. (2000) and Daneri et al. (2005). The nine sutures that were used are; 1. Occipito-parietal; 2. Interparietal; 3. Coronal; 4. Interfrontal; 5. Premaxillary-maxillary; 6. Basioccipito-basisphenoid; 7. Basisphenoid-presphenoid; 8. Squamosal-parietal and 9. Maxillary (Fig. 1). These SIs were used in comparison with estimated ages from dentine tooth sectioning as means of SI calibration and its associated SIs determined by Bester (1990), Kerley and Robinson (1987) and Kerley et al. (2000) in earlier studies of these populations.

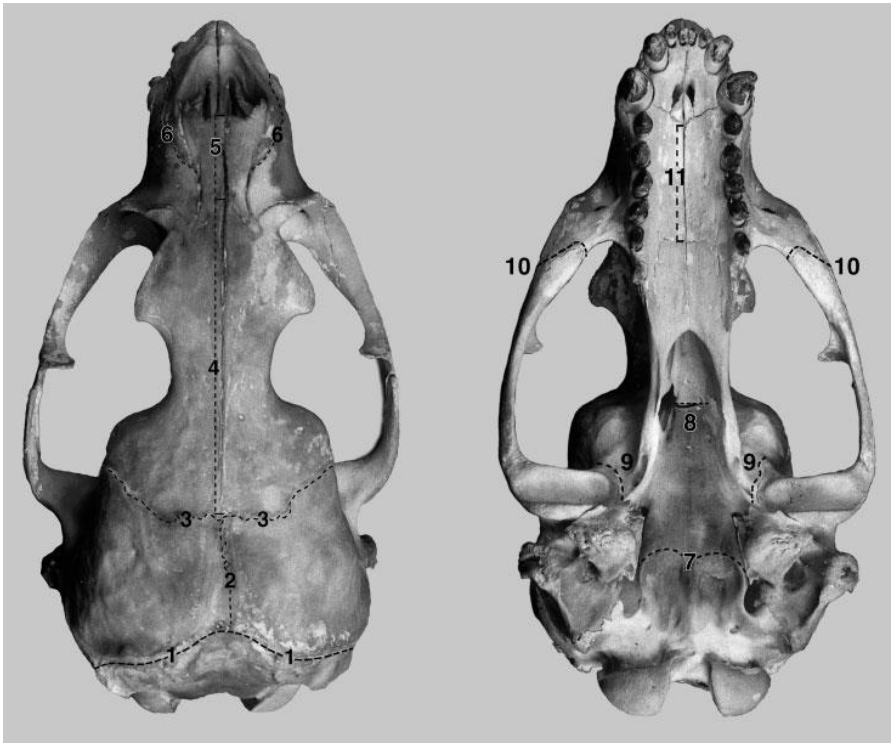


Fig 3.1. Diagram of South African fur seal, *Arctocephalus pusillus* skull (PEM554) indicating the nine sutures (excluding 10 and 11) used in aging the skulls, indicated on the ventral and dorsal aspects of the skulls (taken from Stewardson et al. 2008).

Metrics

The eight skull features that were measured are: IOW, interorbital width; MW, mastoid width; POW, preorbital width; PW1, palate width at postcanine 1; PW3, palate width at postcanine 3; PW5, palate width at postcanine 5; CRW, Calvarial Root Width, and SH, skull height (Fig. 3.2) following Kerley et al. (2000)

The skulls were thoroughly checked for completeness and only intact skulls without fractures or missing features were used. Eight skulls each of *A. gazella* and *A. tropicalis* were analysed accordingly using only the eight variables that previously showed significant differences between the two species (see Kerley and Robinson 1987; Kerley et al. 2000). These variables successfully discriminated the two species (Kerley and Robinson 1987). Measurements of all variables were recorded for each skull to the nearest 0.001 mm, through the photogrammetric procedure described in Chapter 2.

Univariate analysis was done to yield standard statistics (mean, standard deviation, and variance) using Statistica Software 11 package, (StatSoft Inc, South Africa). Further statistical tests were performed for all recorded variables to test for normality (Fig. 3.4). Significance was set at $p < 0.05$. Basic comparisons were performed using *t*-test analysis (Table 3.1). Multivariate statistical analysis (Principal Component Analysis (PCA) was performed to further investigate the differences between the two species using all sets of variables. Principal Component Analysis (PCA) (Fig. 3.3) was used to establish which of the components accounted for larger variations between the two fur seal species. Only the first three principal components were used for comparison in two dimensional projections.

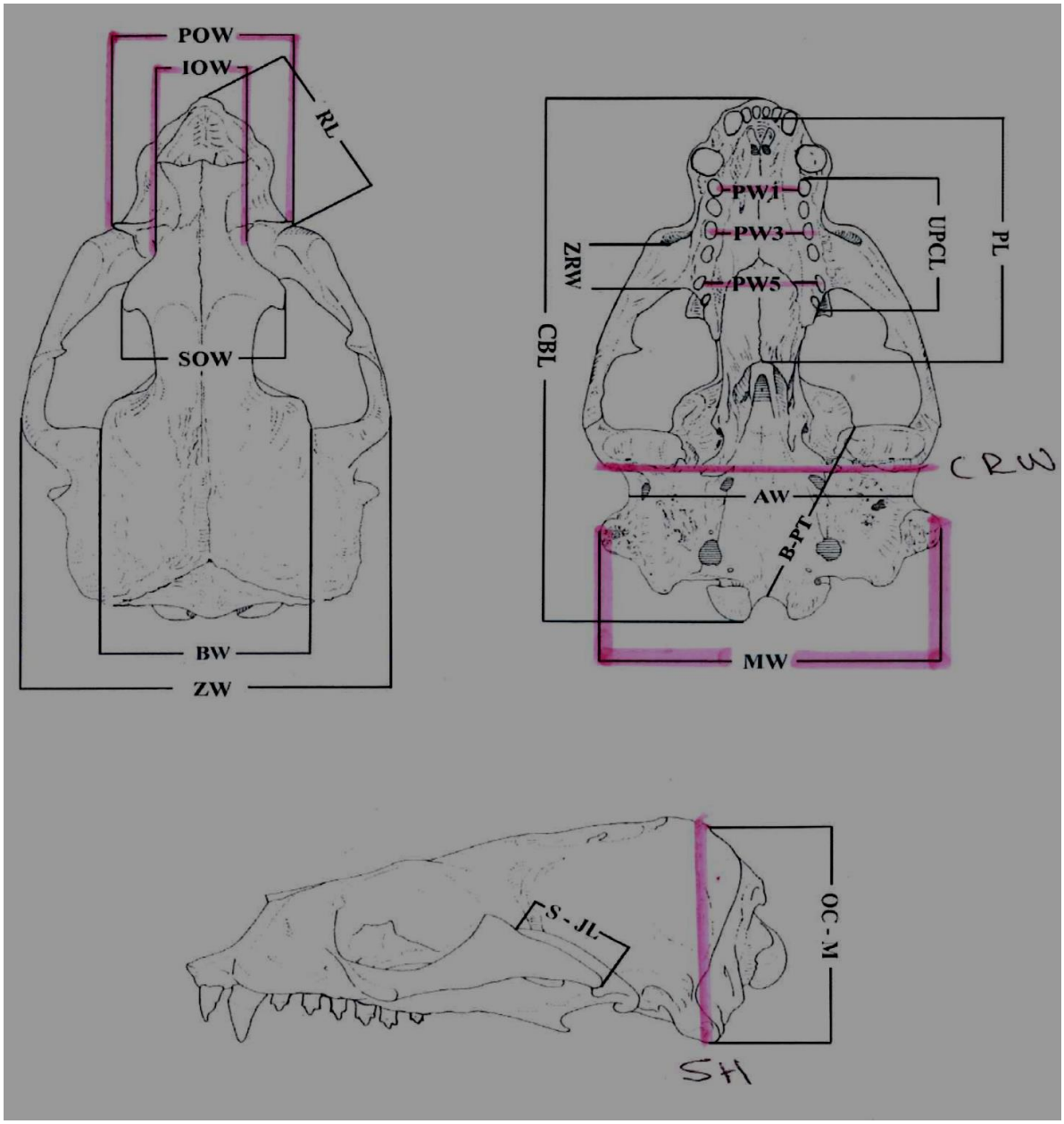


Fig. 3.2. Skull measurements used in this study are highlighted (IOW, interorbital width; MW, mastoid width; POW, preorbital width; PW1, palate width at postcanine1; PW3, palate width at postcanine 3; PW5, palate width at postcanine 5; CRW, Calvarial Root Width, SH, skull height) and is adapted from Daneri et al. (2005).

Results

Almost all measured variables showed clear differences between the two species (Fig. 3.4, Fig. 3.5). The t-tests showed large significant differences (Table 3.1). Two variables showed non-significant difference, namely calvarial root width (p = 0.06) and preorbital process width (p = 0.13). The *A. gazella* skulls were found to be generally larger than *A. tropicalis* for all measured variables. The eigenvalues show that palate width at post-canine 2, palate width at post-canine 3 and mastoid width are the three variables that contributed most to the variation between the two species (Table 3.2 & Fig 3.3).

The principal component analysis (PCA) identified three factors that explained most variance (Table 3.2, Fig. 3.3) factor I, II and III. The first principal component accounted for higher variation (56%) and the principal component two (19%), and principal component three (13%) contributed the least variation of the three components. The data was normally distributed (Fig 3.6), except for two variables (calvarial root width and width at interobital process (Table 3.1,Fig 3.4) and these variables did not show any statistically significant variation between the two species.

Table 3.1. Variation in cranial morphology of adult male Subantarctic fur seals (n=8) and Antarctic fur seals (n=8) based on 8 variables.

Variables	Species	Mean	S.D.	*p* value
Palate width at post-canine 1	*A. gazella*	39.875	3.53	0.038
	A. tropicalis	35.744	3.69	
Palate width at post-canine 3	*A. gazella*	44.543	2.97	0.008
	A. tropicalis	39.369	3.95	
Palate width at post-canine 5	*A. gazella*	49.676	2.51	0.005
	A. tropicalis	43.562	4.57	
Mastoid width	*A. gazella*	142.34	5.32	0.026
	A. tropicalis	133.966	7.89	
Width at Preorbital process	*A. gazella*	60.796	5.79	0.049
	A. tropicalis	53.684	7.36	
Width at Interorbital process	*A. gazella*	42.278	8.21	0.134
	A. tropicalis	33.923	12.38	
Skull height (at tympanic bulla)	*A. gazella*	115.443	6.76	0.02
	A. tropicalis	106.912	6.26	
Calvarial root width	*A. gazella*	125.217	7.55	0.068
	A. tropicalis	119.001	4.7	

Table 3.2. The comparison of Eigenvalues of correlation matrix, and related statistics of all tested variables

	Active variables only			
Value Number	Eigenvalue	Total Variance %	Cumulative Eigenvalue	Cumulative %
1	4.488140	56.10174	4.488140	56.1017
2	1.525728	19.07160	6.013868	75.1733
3	1.086245	13.57806	7.100113	88.7514
4	0.358476	4.48095	7.458589	93.2324
5	0.266944	3.33680	7.725533	96.5692
6	0.146129	1.82662	7.871662	98.3958
7	0.089736	1.12170	7.961398	99.5175
8	0.038602	0.48252	8.000000	100.0000

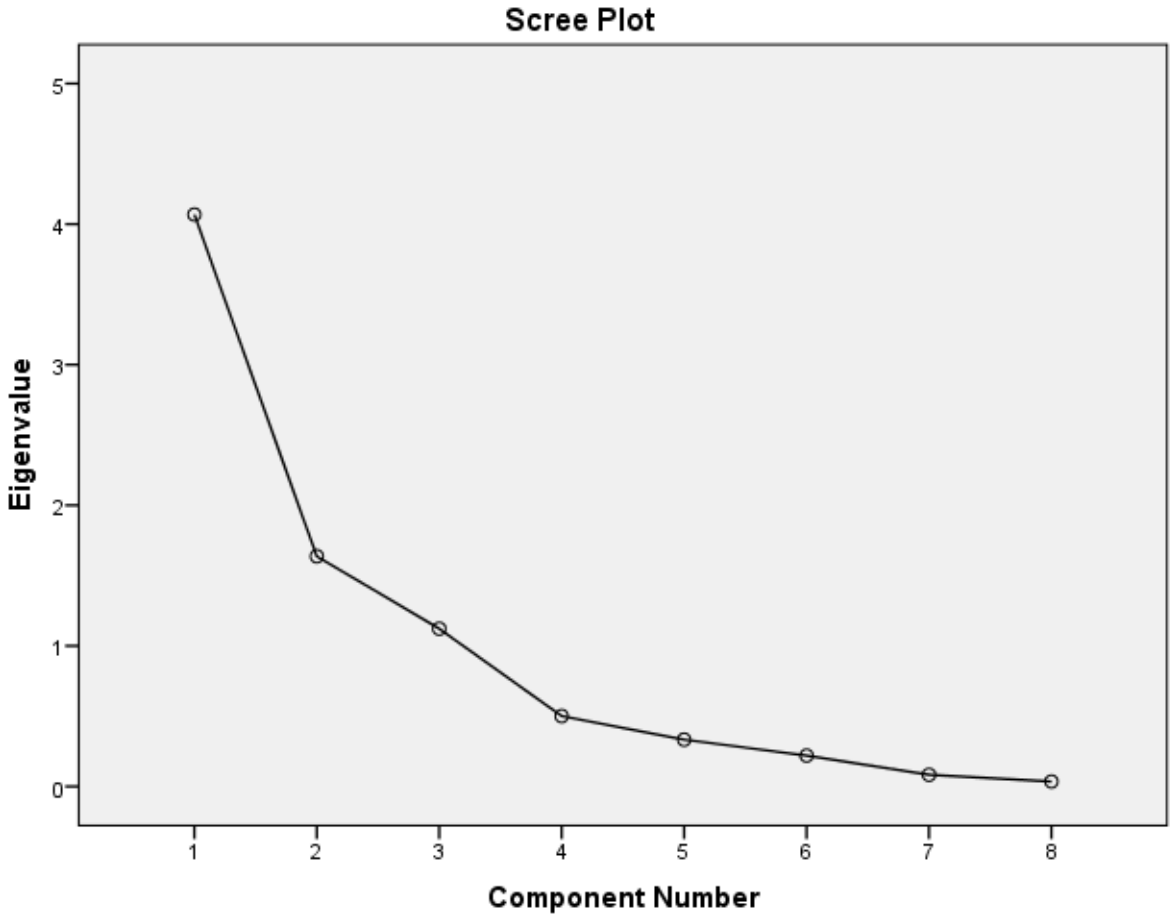
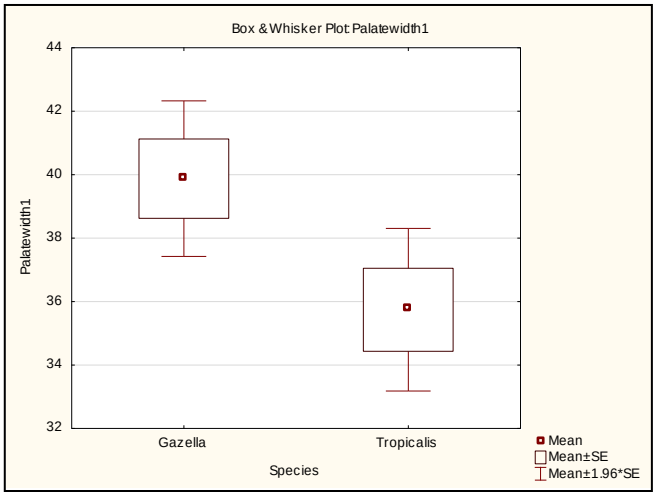
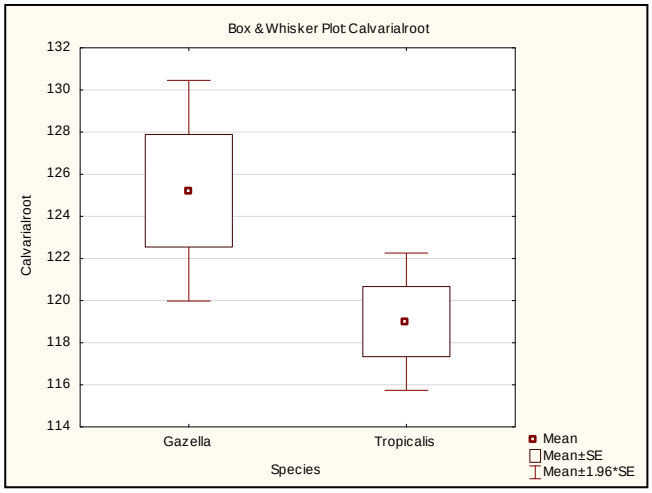
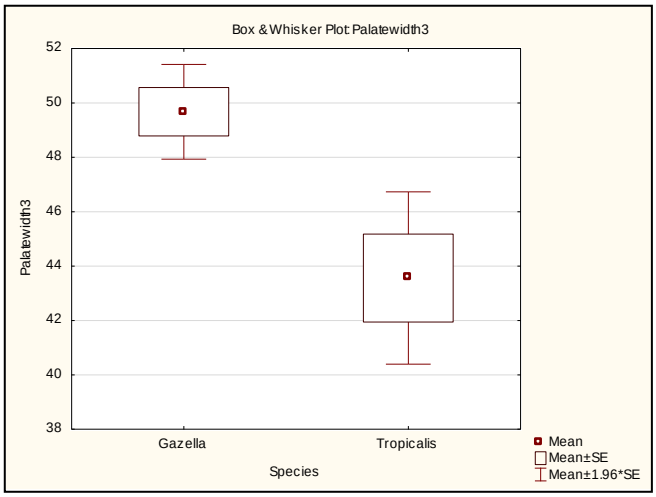


Fig. 3.3. Scree Plot of the components of variation of cranial measurements between the two species, *A. gazella* and *A. tropicalis.*







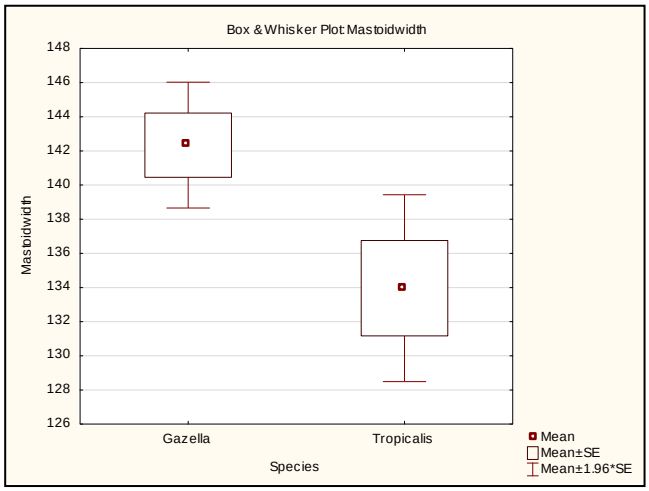
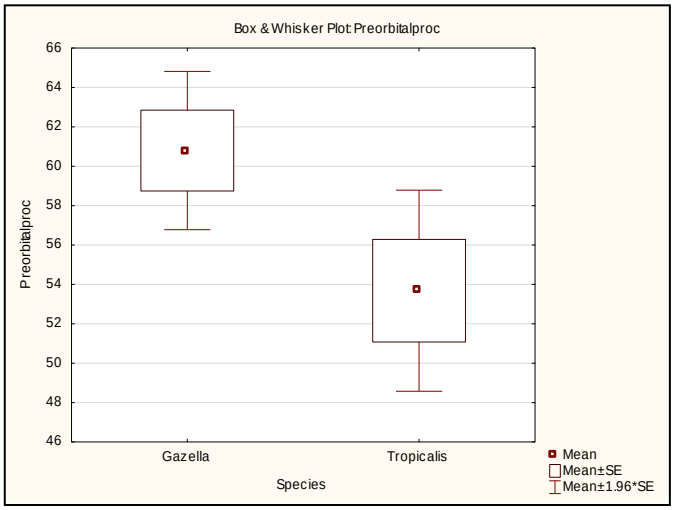
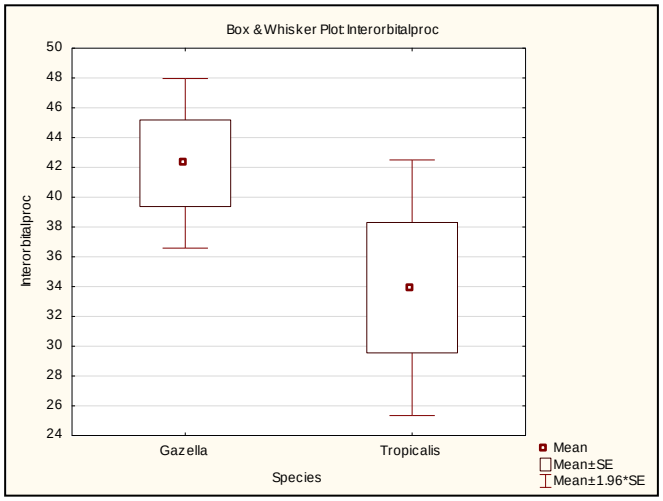
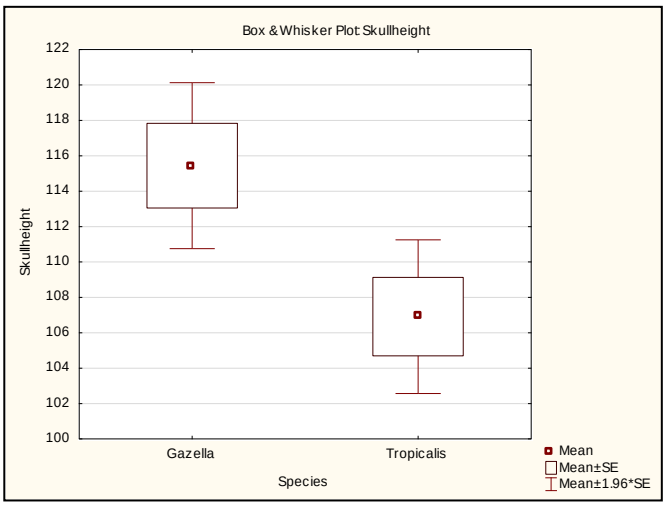


Fig. 3.4. (*continues below*) Box & whisker plots showing the variation of *p*-values of all variables between the adult male skulls of two species, *A. gazella* (n=8) and *A. tropicalis* (n =8).







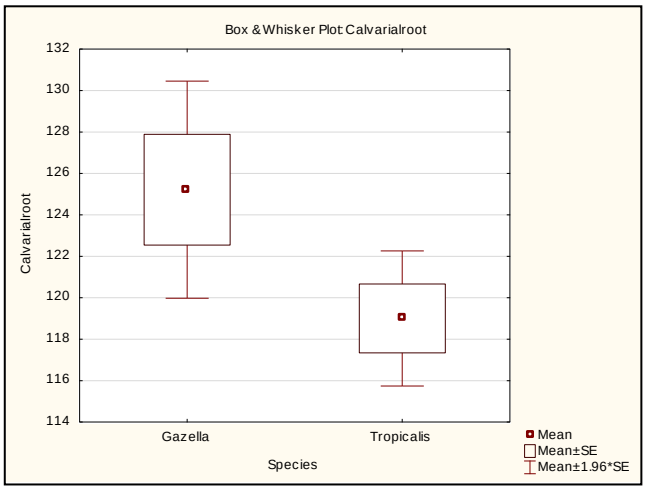


Fig. 3.4. (*Continued*) Box & whisker plots showing the variation of *p*-values of all variables between the adult male skulls of two species, *A. gazella* (n=8) and *A. tropicalis* (n =8).

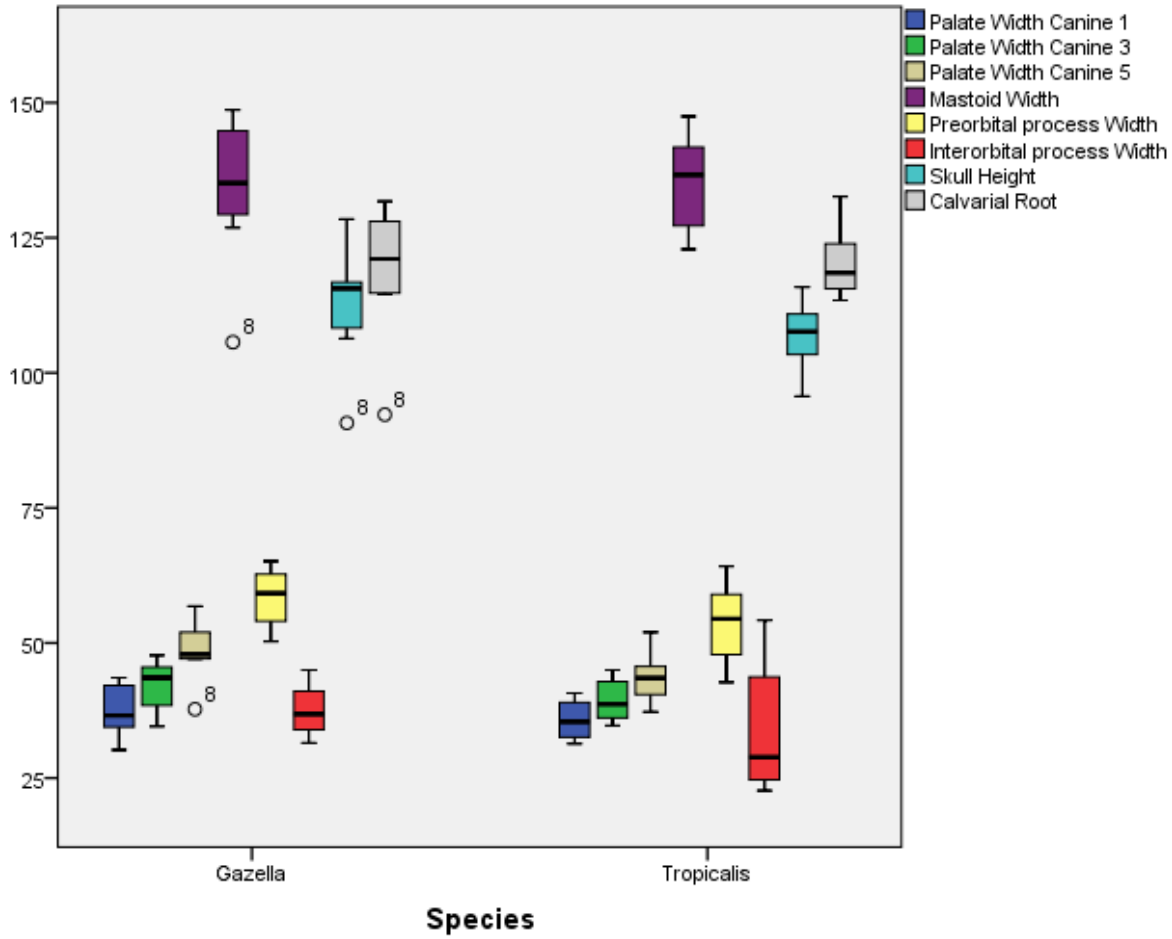
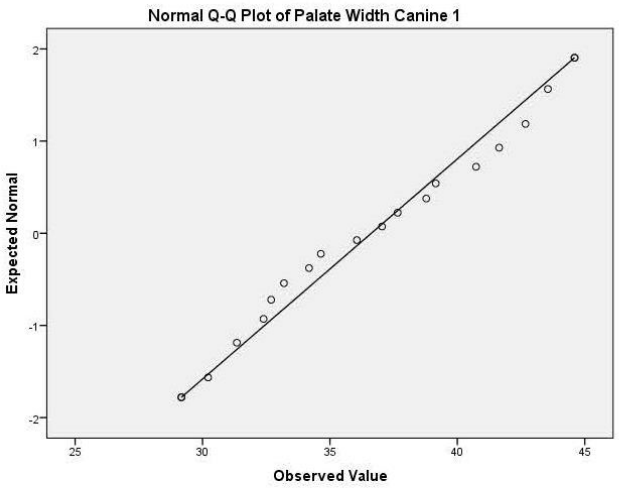
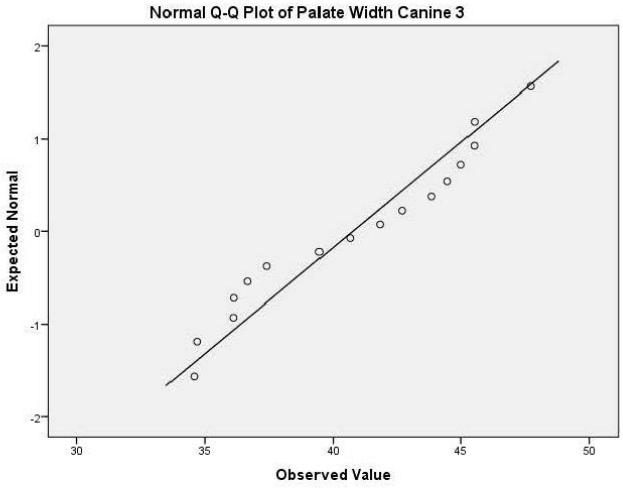
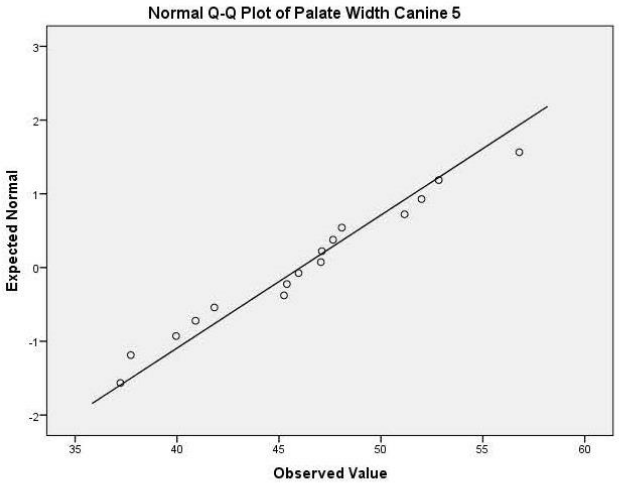
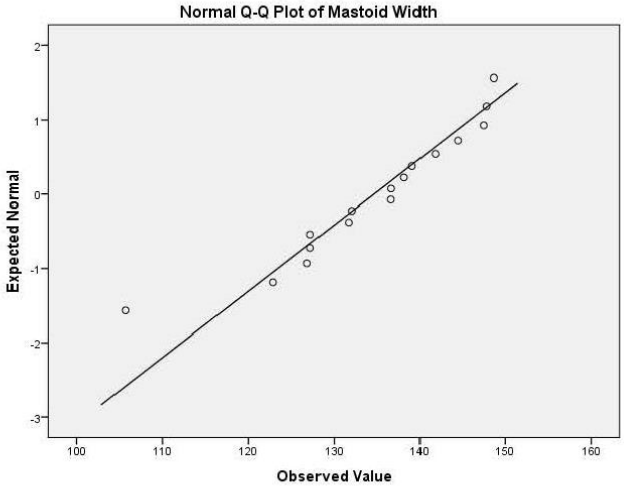


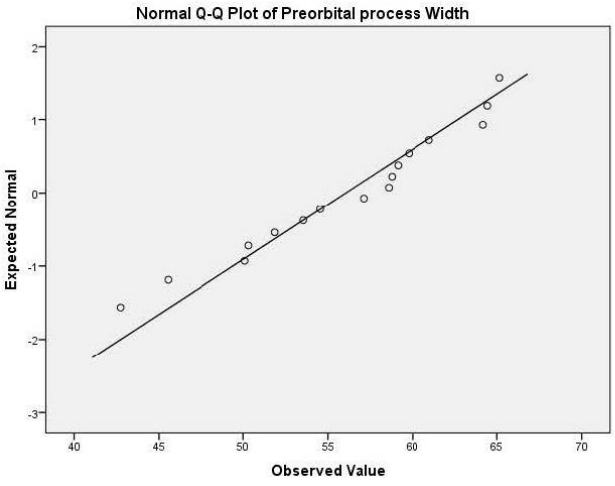
Fig. 3.5. The stem and leaf graph of all the variables used in the discrimination of the two species, *A. gazella* (n=8) and *A. tropicalis* (n =8).

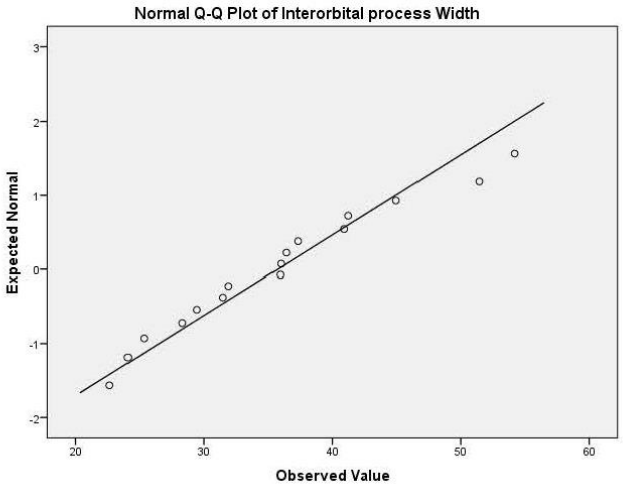

Normal Q-Q Plot of Palate Width Canine 1
Expected Normal
Observed Value


Normal Q-Q Plot of Palate Width Canine 3
Expected Normal
Observed Value


Normal Q-Q Plot of Palate Width Canine 5
Expected Normal
Observed Value


Normal Q-Q Plot of Mastoid Width
Expected Normal
Observed Value


Normal Q-Q Plot of Preorbital process Width
Expected Normal
Observed Value


Normal Q-Q Plot of Interorbital process Width
Expected Normal
Observed Value

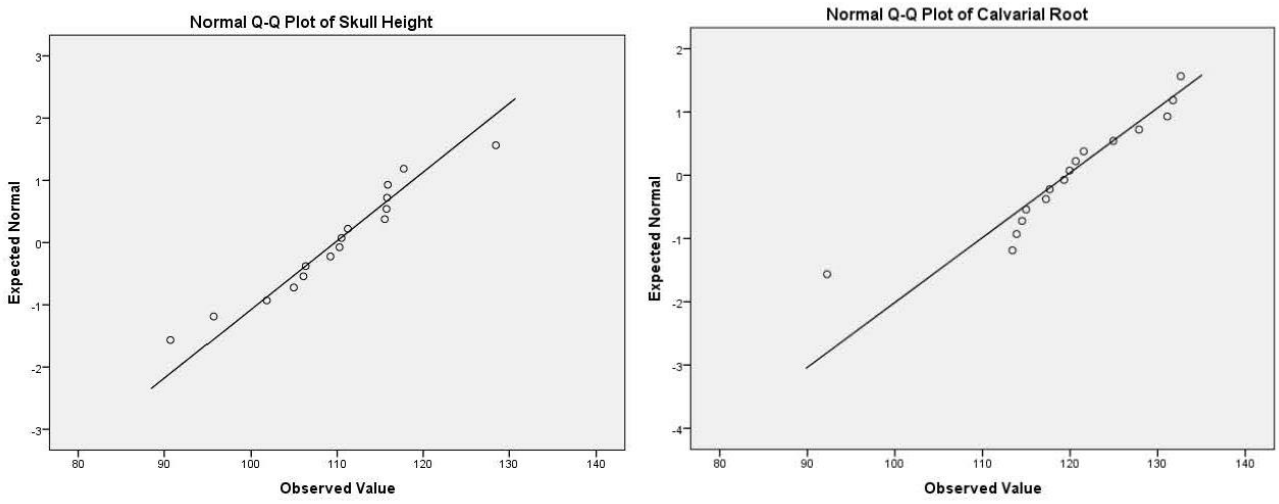


Fig. 3.6. Normality plot of ten measured variables for the discrimination of *A. gazella* and *A. tropicalis* skulls of adult males.

Discussion

The results corroborate that the adult males of the two species are morphologically distinct (Repenning et al. 1971; Condy 1978; Kerley and Robinson 1987). The *t*-tests (Table 3.1), and principal component analysis (PCA) (Table 3.2, Fig. 3.3) of the data all show that adult male skulls of *A. gazella* and *A. tropicalis* are different, adult *A. gazella* males being larger than *A. tropicalis* (Repenning et al. 1971; this study) (Fig. 3.4). Despite historical factors that could lead to population bottlenecking and inbreeding, such as sealing, local adaptation, possible genetic drifts and thus low population variation, all tested cranial measurements show great difference between the two species. However, three variables contributed more to the differences than the other five. The inter-orbital process width and calvarial root width varied little between the two species (Fig 3.4). However the observed variations in this chapter may be attributed to low sample size. Although the significant variations observed in this study, would require a large sample size to validate our deductions. Kerley and Robinson (1987) distinguished the two species based on all 18 of their recorded measurements, using caliper on skulls from each species. Measurements (calipers and those done using PMSc® software on 3D constructions) of skulls of adult males confirm that the two species are morphologically different.

Conclusion

I combined morphological analysis and photogrammetric analyses and demonstrate significant morphological differences between skulls of adult male *A. gazella,* and *A. tropicalis.* Despite our small sample size, our results corroborate earlier studies (Repenning et al. 1971; Condy 1978; Kerley and Robinson 1987) that there is a significant size difference between the two species and therefore that they are separable by morphological means (Kerley and Robinson 1987; this study). Furthermore, it is also evident that photogrammetry is successful in distinguishing the two species. Therefore 3D photogrammetry through the aid of PMSc® could successfully be used in craniometrics as a most efficient and reliable tool for cranial measurements and possibly for other somatic measurements.

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CHAPTER 4

Inter-population craniometrics of adult male Subantarctic fur seals (*Arctocephalus tropicalis*)

Abstract

Geographic variation in animal body size is a common phenomenon among animals. There is a graded latitudinal difference in adult body size of Subantarctic fur seals *Arctocephalus tropicalis*, but the skull morphometrics of adult males from two different populations were similar. Photomodeler Scanner® (PMSc®) three-dimensional (3-D) modeling software was used to investigate possible geographic differences in the craniometrics of Subantarctic fur seal populations at Gough Island (40°29'S, 09°54'E) and Marion Island (46°54'S, 37°45'E) and to test whether Subantarctic fur seal skulls conform to the Bergman rule. Ten metric variables were recorded from high resolution 3D skull models of adult male Subantarctic fur seals *A. tropicalis* from Marion Island (n = 54) and Gough Island (n = 31). No statistically significant craniometric differences between these two Subantarctic fur seals populations were detected in any tested variables of adult male skulls. Therefore Marion Island and Gough Island populations cannot be discriminated using skull linear measurements, and adult male Subantarctic fur seals do not conform to Bergmann's rule.

Introduction

Geographic variation in body size is a common phenomenon among animals (Yom-Tov and Geffen 2006). Geographic variation in size probably results from the interaction of local environmental conditions and genetic differences among populations (Caughley 1994). Biological variation can be represented at two levels, intra-specific variation, and interspecific variation (Mayr 1963). Geographic variation in environmental conditions is a major ecological factor involved in evolutionary diversification and it has sparked continued interest from macro-ecologists, bio-geographers, and conservationists (Margalef 1955; McNab 1971; Peters 1983; Calder 1984; Brown and Nicoletto 1991; Crooks 2002; Meiri and Thomas 2007; Olden et al. 2007; Greve et al. 2008). The morphology of an organism can be affected by the environmental conditions in a given geographical locality, bring about co-variation between phenotypic traits as mentioned by Pincheira-Donoso et al. (2008). It is commonly assumed that differences in groups have adaptive significance (Radinsky 1984). Morphology is known to exhibit substantial variation in relation to climate gradient. There is a wealth of studies aimed at unveiling how abiotic and biotic factors produce patterns of variations, this lead to introduction of several ecological pattern ideas, such as the popular Bergmann's Rule (Mayr 1956). Bergmann's Rule states that "Races from cooler climates tend to be bigger in species of warm-blooded vertebrates, than races of the same species living in warmer climates" (Bergmann 1847; Brunner et al. 2002). Morphological variation studies have been an integral part of systematics and taxonomy, and aided in classification of species (Mayr 1963). Morphological variation might also give some information on functional aspects of importance in species divergent differentiation.

The Subantarctic fur seal, *Arctocephalus tropicalis,* is widely distributed throughout the southern hemisphere (Goldsworthy and Shaughnessy 1989; Georges et al. 2000). They have, since cessation of sealing, recolonized most of their native breeding grounds (Hofmeyr et al. 2006). The species breeds on temperate islands in the south Atlantic and Indian Oceans (Guinet et al. 1994). The largest populations are found at Amsterdam, Gough, and the Prince Edward Islands (Marion Island and Prince Edward Island) (Guinet et al. 1994). Generally the Subantarctic fur seal individuals from Marion and Gough islands are indistinguishable in appearance

(Kerley et al. 2000). There is evidence of a graded latitudinal difference in adult body size of Subantarctic fur seals (Bester and Van Jaarsveld 1994) but the skull morphometrics of adult males from the two different populations were similar (Kerley et al. 2000). The purpose of the study was to re-evaluate the earlier findings (Kerley et al. 2000) of Subantarctic fur seals at Gough Island (46°54'S, 37°45'E) and Marion Island (40°29'S, 09°54'E) by using a different measurement approach. We further aimed at creating accurate high resolution three-dimensional (3D) models of the skulls to render caliper measurements obsolete and to create a digital museum.

Materials and Methods

Subantarctic fur seal skulls that were collected over the period 1977 to 2008, from Gough Island (46°54'S, 37°45'E) and Marion Island (40°29'S, 09°54'E) by various scientists were used in this study. A total of 85 adult male specimens of Subantarctic fur seal skulls were examined (51 from Marion Island; 34 from Gough Island).

Study area: Prince Edward Islands (PEIs)

The Subantarctic PEIs are volcanic in origin (McDougal 1971). PEIs are comprised of the larger (296 km^2) Marion Island (46° 54' S, 37° 45' E) and Prince Edward Island (size) (46° 13' S, 37° 15' E), which are 21km apart (Ansorge and Lutjeharms 2003). Marion Islands support one of the world's largest Subantarctic populations, with approximately 48 000 individuals (Bester 1990, Hofmeyr et al 1997).

Study area: Gough Island

Gough Island (40°21′S, 9°53′W), in the central South Atlantic Ocean, is located approximately 3000km from both South Africa and South America and ~350 km southeast of Tristan da Cunha (Cooper and Ryan 1994). Gough, an uninhabited volcanic mountainous island, is 91 km^2 in size (Wace and Holdgate 1976). The temperate Gough Island lies well north of the Antarctic Polar Front in the cool temperate zone of the South Atlantic Ocean (Höflich 1984). Approximately 48 000 Subantarctic fur seals inhabit 200 000 Island (Bester 1990, Hofmeyr et al 1997).

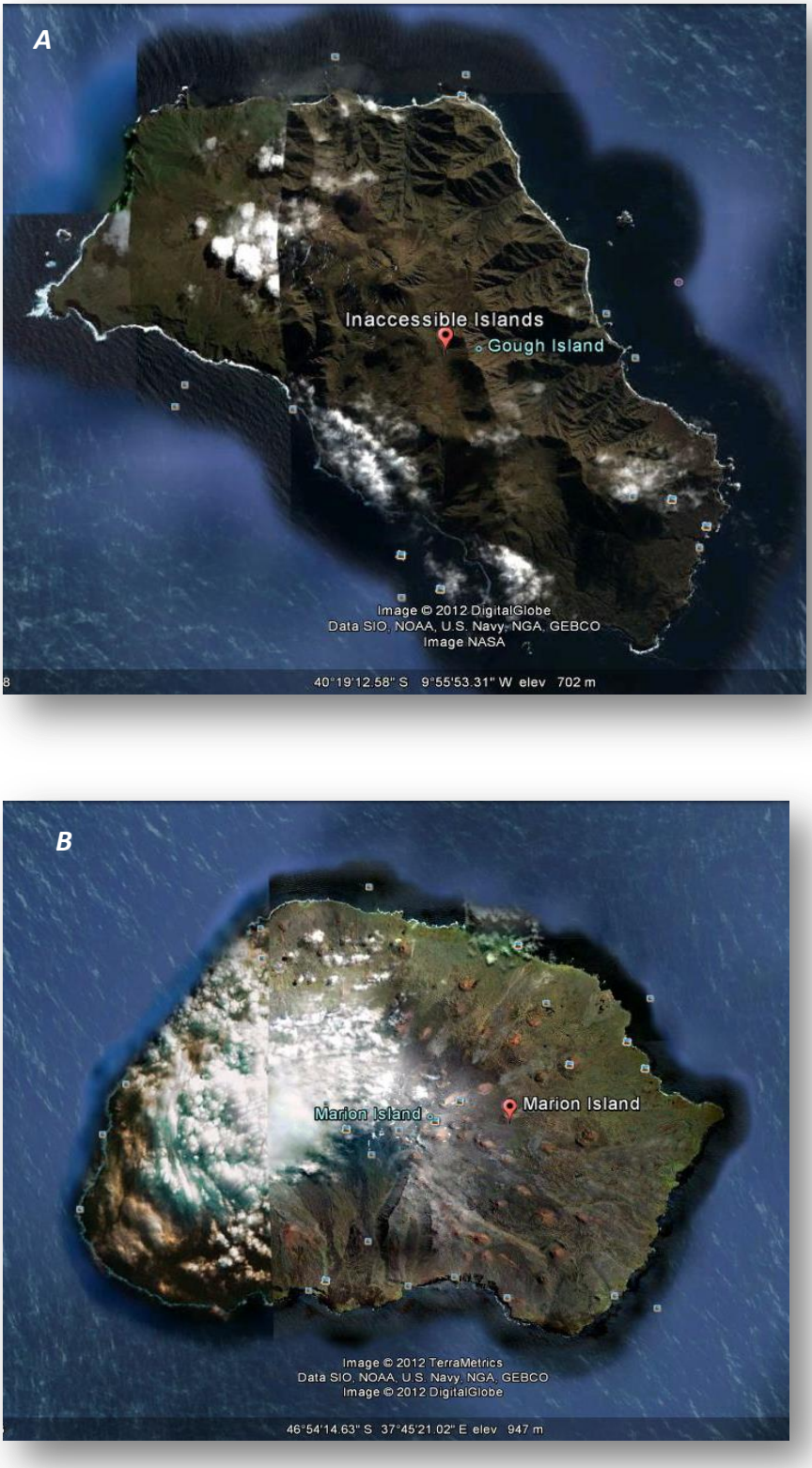


Fig. 4.1. Map presenting the two studied geographic areas, as the localities of the origin of the specimens, A) Gough Island and B) Marion Island (Google Earth 2013).

Material examined

Collection

Only adult males were included in the study, the sex was determined at collection and specimens were labelled. The male Subantarctic fur seals were shot with a 0.22 rifle from close range at breeding, non-breeding and idle colony sites as explained in Bester (1982) at Gough Island and Marion Island. The sample also included animals which had died of natural causes. The skulls that were used were collected in the period 1977-2008 and aged based upon incremental lines in the dentine of sectioned canines (Bester 1990) and from suture indices (see below), together with external morphological characteristics at the time of shooting.

The skulls were de-fleshed and boiled in water until the flesh could be removed easily. Skulls were then washed with mild detergent mixed in water and air dried at room temperature.

Age determination (Suture Index, SI)

Specimens were aged on the basis of suture indexing (SI) of Sivertsen (1954). Nine cranial sutures (Fig. 4.2) from skulls were assigned a value of 1 to 4, according to the degree of closure (1 = suture fully open; 2 = more than half open; 3 = suture more than half closed; 4 = suture fully closed), which translates into an index (SI), ranging from 9 (all nine sutures fully open) to 36 (all nine sutures fully closed). These values were then added together to give a total suture index (SI), as used in Sivertsen (1954), Kerley and Robinson (1987), Brunner (1998), Kerley et al. (2000), and Stewardson et al. (2008). The nine sutures that were used are; 1. Occipito-parietal; 2. Interparietal; 3. Coronal; 4. Interfrontal; 5. Premaxillary-maxillary; 6. Basioccipito-basisphenoid; 7. Basisphenoid-presphenoid; 8. Squamosal-parietal and 9. Maxillary (Fig. 1). These SIs were applied to delineate adult males from subadults using the relationship between SI and estimated ages from tooth sections (Fig 4.11) as determined by Bester (1990), Kerley and Robinson (1987) and Kerley et al. (2000) in earlier studies of these populations. The dentine tooth sectioning data which is available in literature (Bester 1990) and was used to calibrate the SIs data. The confounding effect of age variation was removed by including only adults, $\geq$9 years old, the age at which adult males are at/past the inflection point of skull

(condylobasal) and body (Standard Length) growth (Bester and Van Jaarsveld 1994). The SI of skulls ≥22 corresponding to >9 years was considered for analyses.

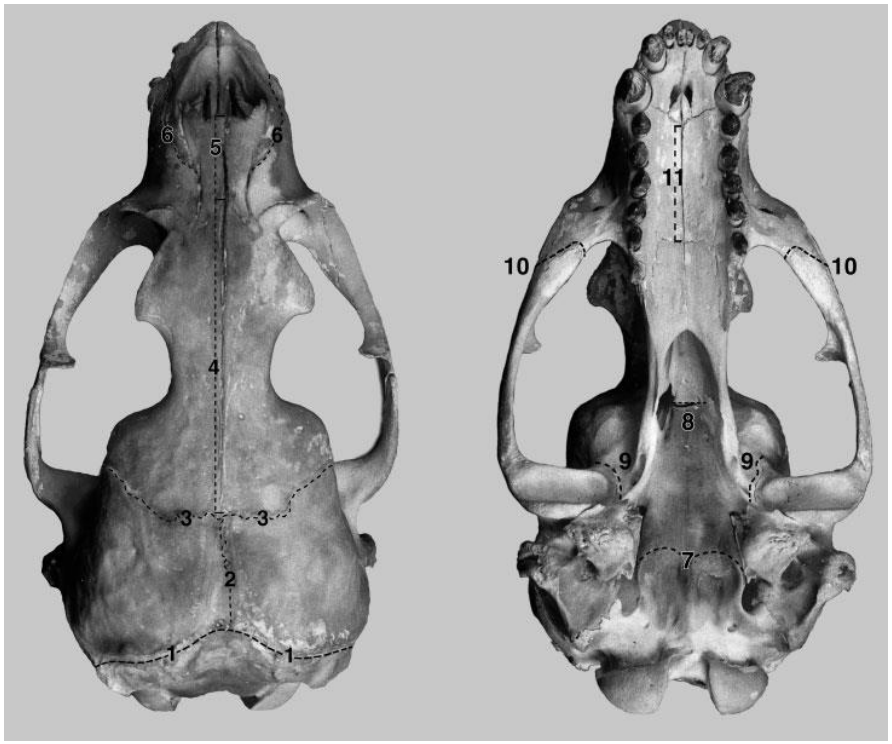


Fig: 4.2. Diagram of a South African fur seal, *Arctocephalus pusillus pusillus,* skull showing the position of sutures examined in this study excluding sutures 10 and 11 (Used as an example) (Stewardson et al. 2008)

3-D Modelling

Photomodeler Scanner® (EOS systems, Vancouver) three-dimensional (3-D) modelling software was used to produce accurate and high resolution 3D models of Subantarctic fur seal skulls. Using a pre-calibrated camera Kodak Easy share C 195 camera with 14 megapixels (Fig. 4.3), photos were taken around the skull following the Smartmatch® functionality guidelines (Fig 4.4). For detailed step by step procedure (see Chapter 2 and Photomodeler help files). The 3D skull models were produced as described in Chapter 2, and point to point measurements recorded to the nearest 0.01 mm using the software's own Measurement tool®.

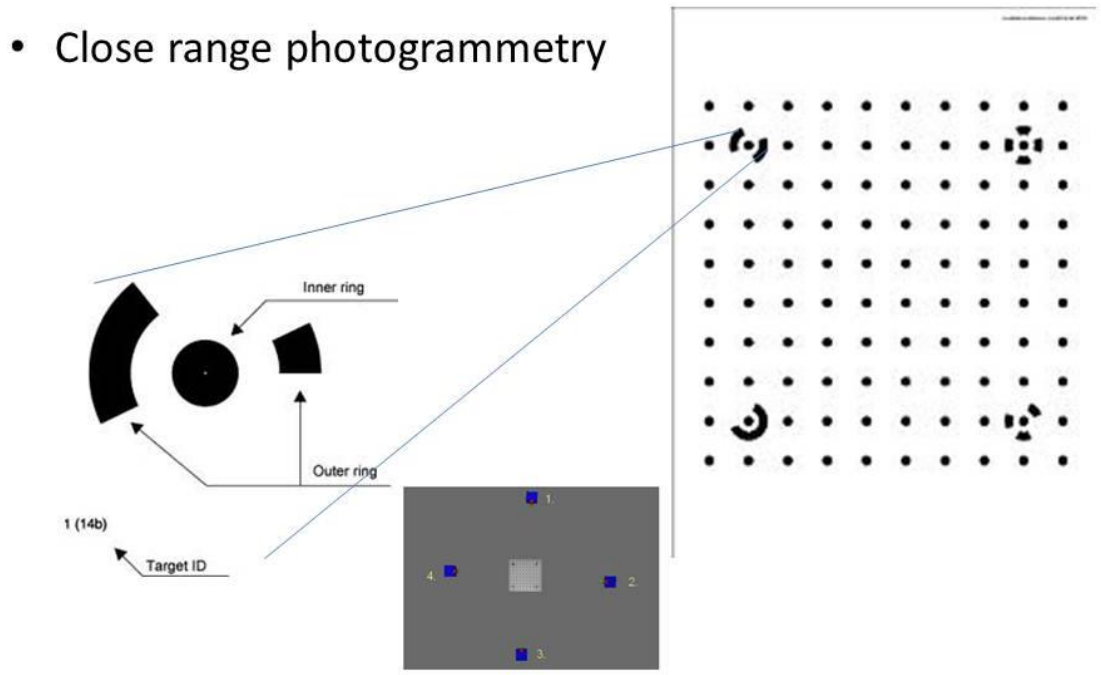


Fig. 4.3. Calibration sheet for calibrating the cameras used in the study.

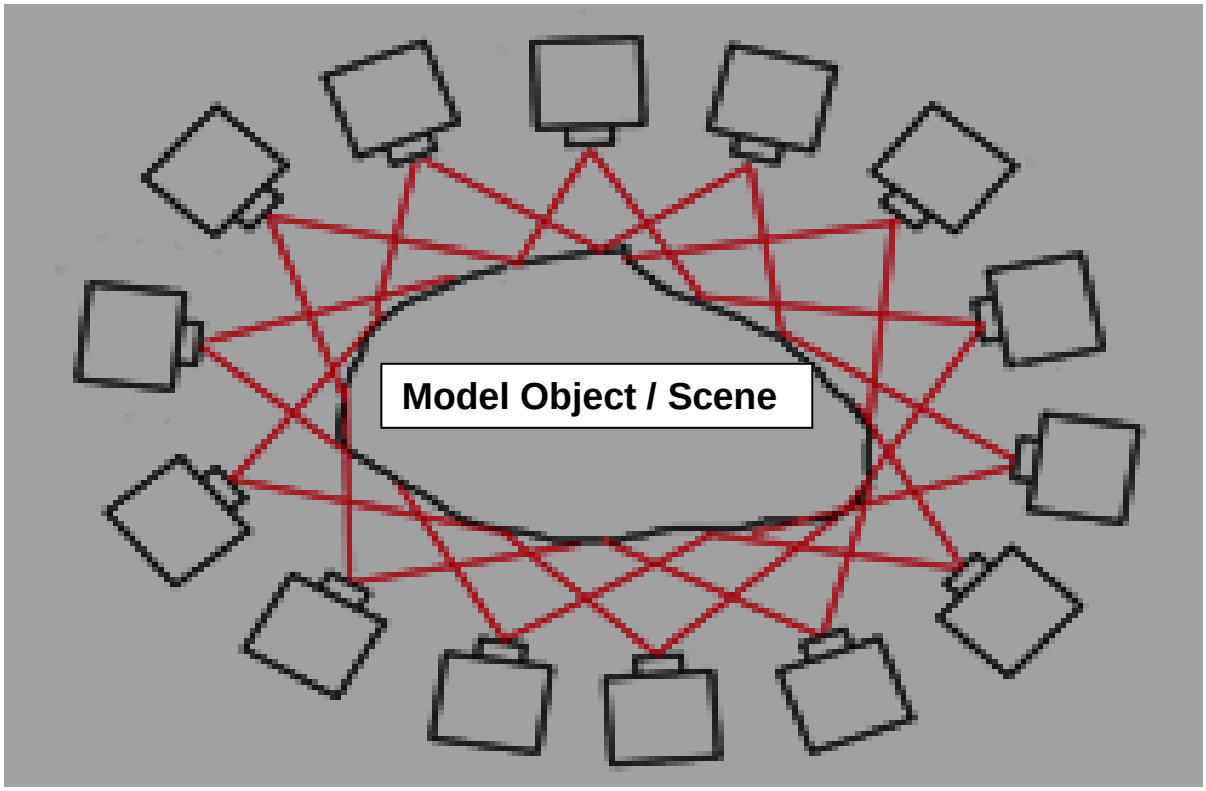


Fig. 4.4. Schematic view of the camera arrangement around the object of interest for taking photographs for Smartmatch® 3D modelling (Photomodeler help files).

Smartmatch® functionality uses a fully automated method which marks and references points on natural features and generates 'Smart Points' then orients and processes the photos to provide fully automatic project set up and orientation for non-targeted projects (Fig 4.5).

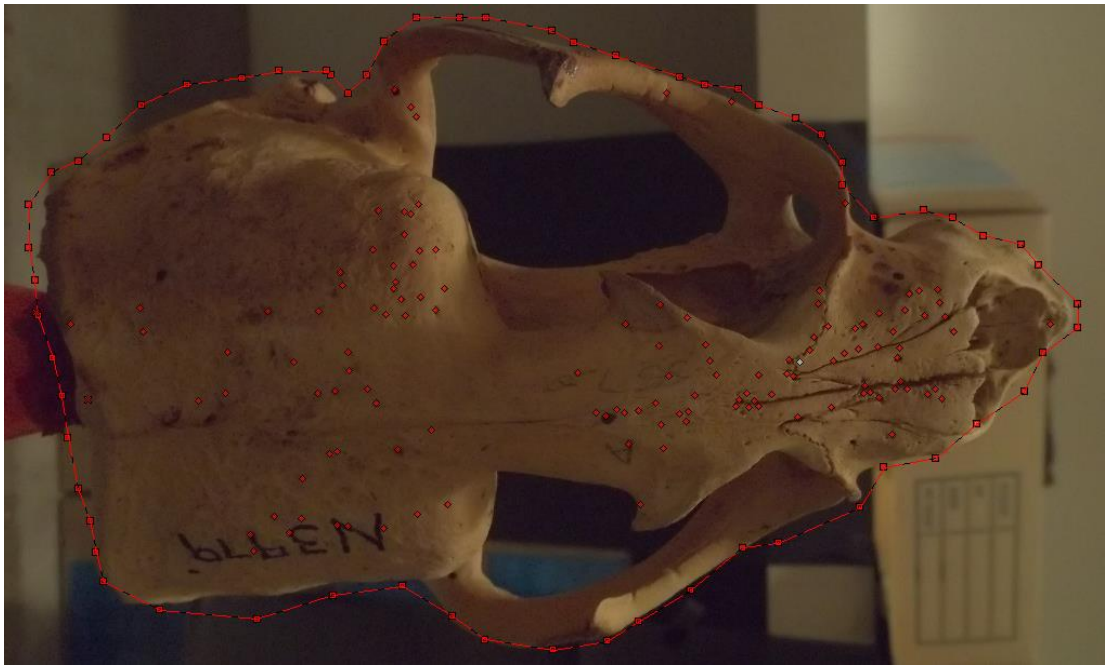


Fig. 4.5. Skull image for measurements with 3D Smartmatch® points.

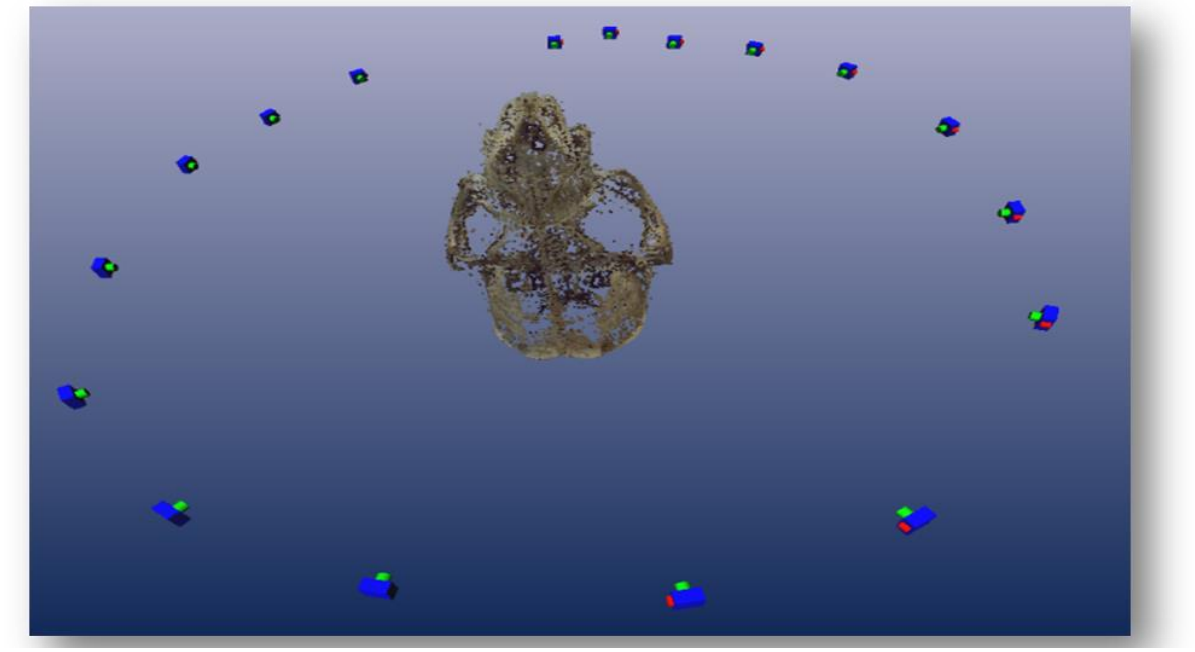


Fig. 4.6. Camera placement setup for photograph acquisition and 3D skull configuration Metrics.

The 10 skull parameters (Fig.4.7) that were measured are mastoid width (MW), interorbital width (IOW), preorbital width (POW), palate width at postcanine 1 (PW1), palate width at postcanine 3 (PW3), palate width at postcanine 5 (PW5), upper postcanine length (UPCL), palatal length (PL), skull height (SH) and Calvarial root (CR), following Kerley et al. (2000).

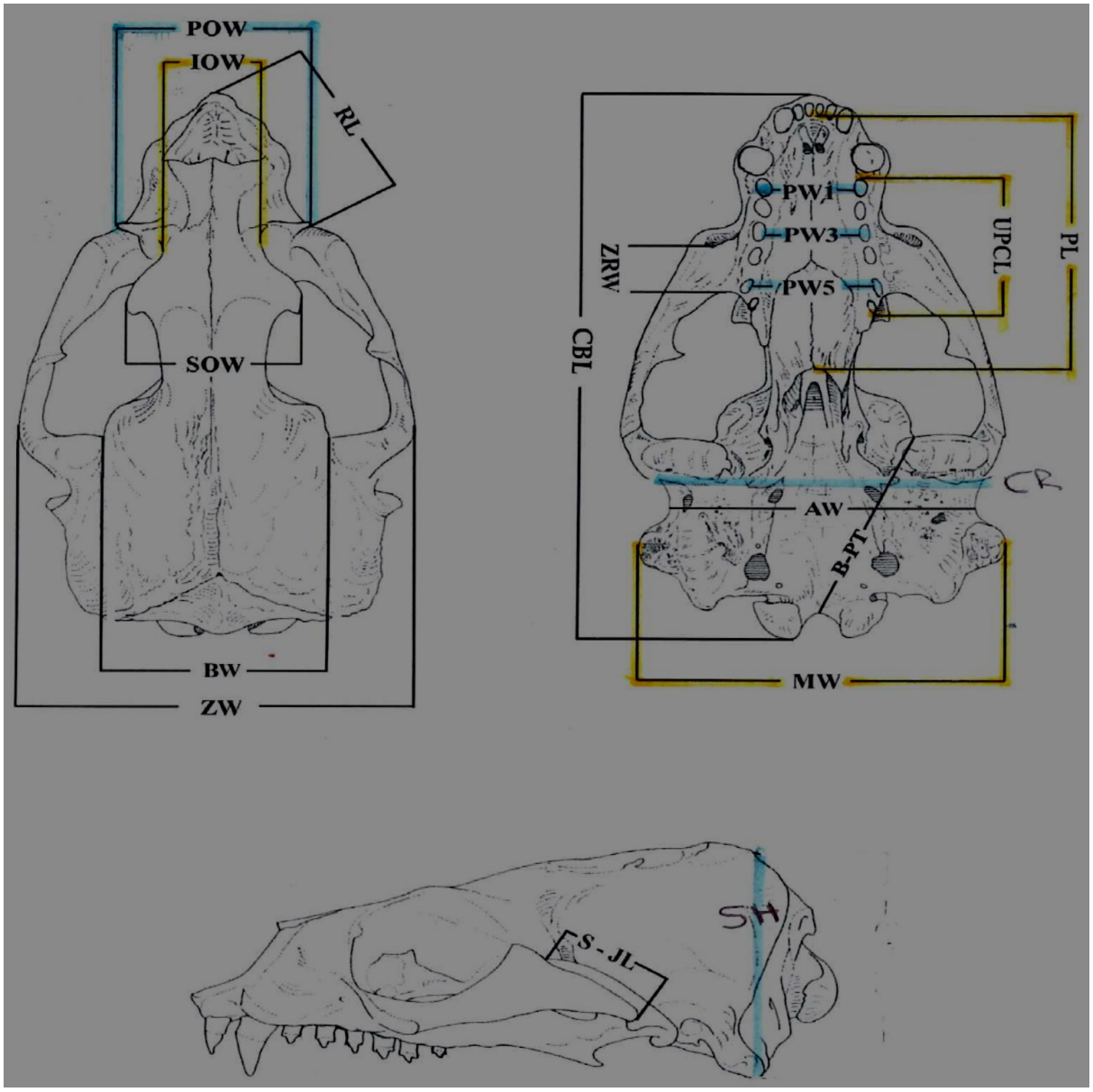


Fig 4.7. Skull measurements used in this study (highlighted - IOW, interorbital width; MW, mastoid width; PL, palatal length; POW, preorbital width; PW1, palate width at postcanine1; PW3, palate width at postcanine 3; PW5, palate width at postcanine 5; UPCL, upper postcanine length; SH, skull height) adopted from Daneri et al. (2005).

Analysis

Basic statistics were performed using the Statistica® 11, (StatSoft, Inc, South Africa) software package. Normality in data distribution was tested using Shapiro-Wilk normality test Multivariate statistical analyses were performed, and Principal Component Analyses (PCAs) and Discriminant Analyses (DA) were used to analyse for the existence of differences or similarities between the two populations. The data that was not normally distributed was first transformed before the PCA was performed. The Principal Component Analyses (PCAs) were applied to investigate whether the two populations were craniometrically distinct or not. Discriminant analyses (DA), was used to determine the nature of the differences between the populations. Ten metrics were all used as depended variables.

Results

To demonstrate whether a significant variation in skull morphology exists between Subantarctic fur seal populations from Gough Island (n = 31) and Marion Island (n = 54) using a new approach, sample size was increased over that available to Kerley and Robinson (1987) and Kerley et al. (2000). A total of 10 skull measurements recorded were computed for variance analysis, (Table 4.1) and were found to be similar. No significant differences between the two populations exist (Table 4.2) despite individual skulls from Gough Island population being generally larger in size than individuals from the Marion Island population.

The results of the PCA (Fig. 4.8) showed that PC1 accounted for 72% of variation, and PC2 10% of variation between the two populations. The PCA results do not show any detectable difference between the two populations on both components, PC I with an Eigen value of 7.2 and PC II Eigenvalue of 1.0. The data was subjected for normality tests (Fig. 4.9), to ensure that the data is normally distributed, and most variables were not normally distributed and were transformed. However, even after transformation no variations were detected. The PCI accounted for 73.4% and PC II accounted for 9.9% of variation with Eigen values of 7.33 and 0.99 respectively.

The DA results (Table 4.3) allowed the use of only five variables which revealed that the adult males of two populations are similar. The two populations therefore cannot be differentiated based on linear craniometrics

Table 4.1. The mean and standard deviation (SD) of each of the measured variables of adult male skulls from Marion and Gough islands.

Report

Location		Palatal Length	Palate width at molar 1	Palate width at molar 3	Palate width at molar 5	Mastoid width	Preorbital Process Width	Inter Orbital Process width	Skull Height	Upper Post canine Length	Calvarial Root Width
Marion	Mean	70.32476	28.9587	32.44878	36.65146	91.06935	36.35409	16.47059	74.01022	44.27909	86.31843
	N	54	54	54	54	54	54	54	54	54	54
	SD	8.1658	2.68817	2.757308	2.801511	13.49386	4.573717	3.531307	14.15616	5.628274	12.73295
Gough	Mean	72.8931	28.855	32.31529	36.27726	92.38368	36.72319	16.10913	75.52513	45.84487	89.16223
	N	31	31	31	31	31	31	31	31	31	31
	SD	9.640639	3.133296	3.145767	3.215781	13.52733	4.284528	3.33914	16.66537	5.973094	11.96535
Total	Mean	71.26145	28.92088	32.40009	36.51499	91.54869	36.48871	16.33876	74.56272	44.85014	87.35558
	N	85	85	85	85	85	85	85	85	85	85
	SD	8.764256	2.84046	2.887106	2.945868	13.44041	4.448247	3.446851	15.03895	5.77095	12.46287

Table 4.2. ANOVA test results for differences between skulls of adult male Subantarctic fur seals from Marion and Gough islands and the statistical significance of the transformed data.

Variable	*F*	*Sig.*	Variable ^{Transformed}	F^{log}	$Sig.^{log}$
Palatal Length	1.705	0.195	LogPL	1.575	0.213
Palate width at molar 1	0.026	0.872	LogPW1	0.054	0.817
Palate width at molar 3	0.042	0.839	LogPW3	0.069	0.793
Palate width at molar 5	0.315	0.576	LogPW5	0.357	0.552
Mastoid width	0.187	0.667	LogMW	0.193	0.662
Preorbital Process Width	0.134	0.715	LogPOPW	0.163	0.688
Inter Orbital Process width	0.215	0.644	LogIOPW	0.175	0.676
Skull Height	0.198	0.658	LogSH	0.088	0.768
Upper Post canine Length	1.458	0.231	LogUPCL	1.424	0.236
Calvarial Root Width	1.026	0.314	LogCRW	1.031	0.313

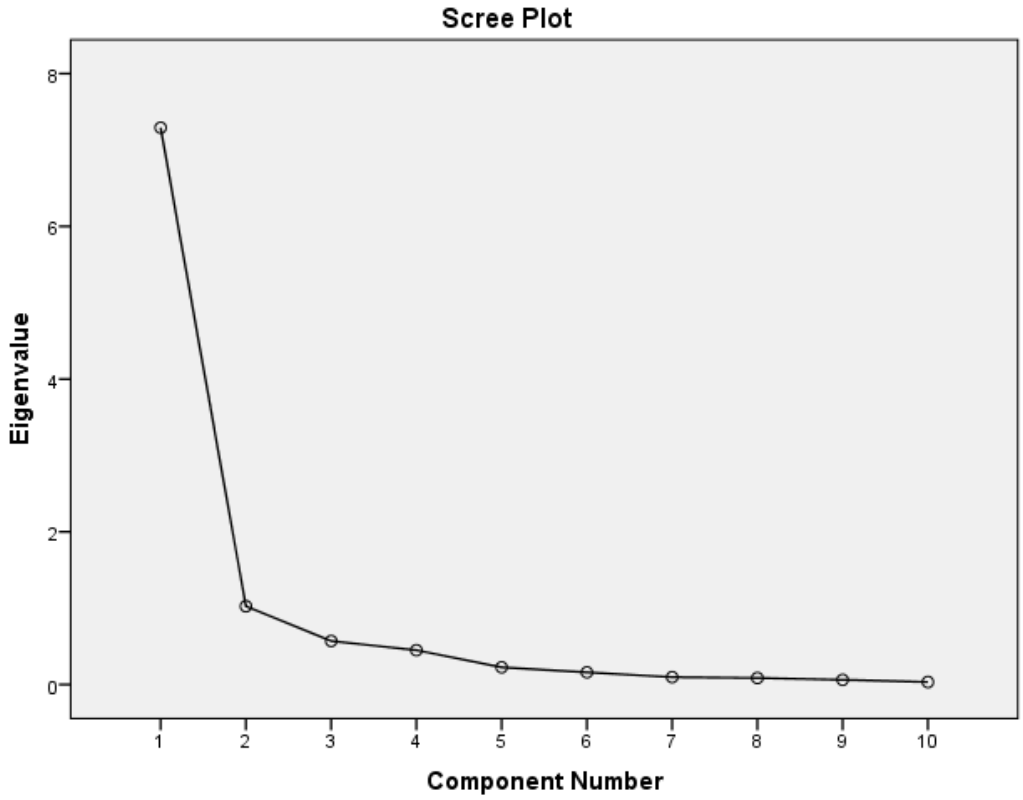
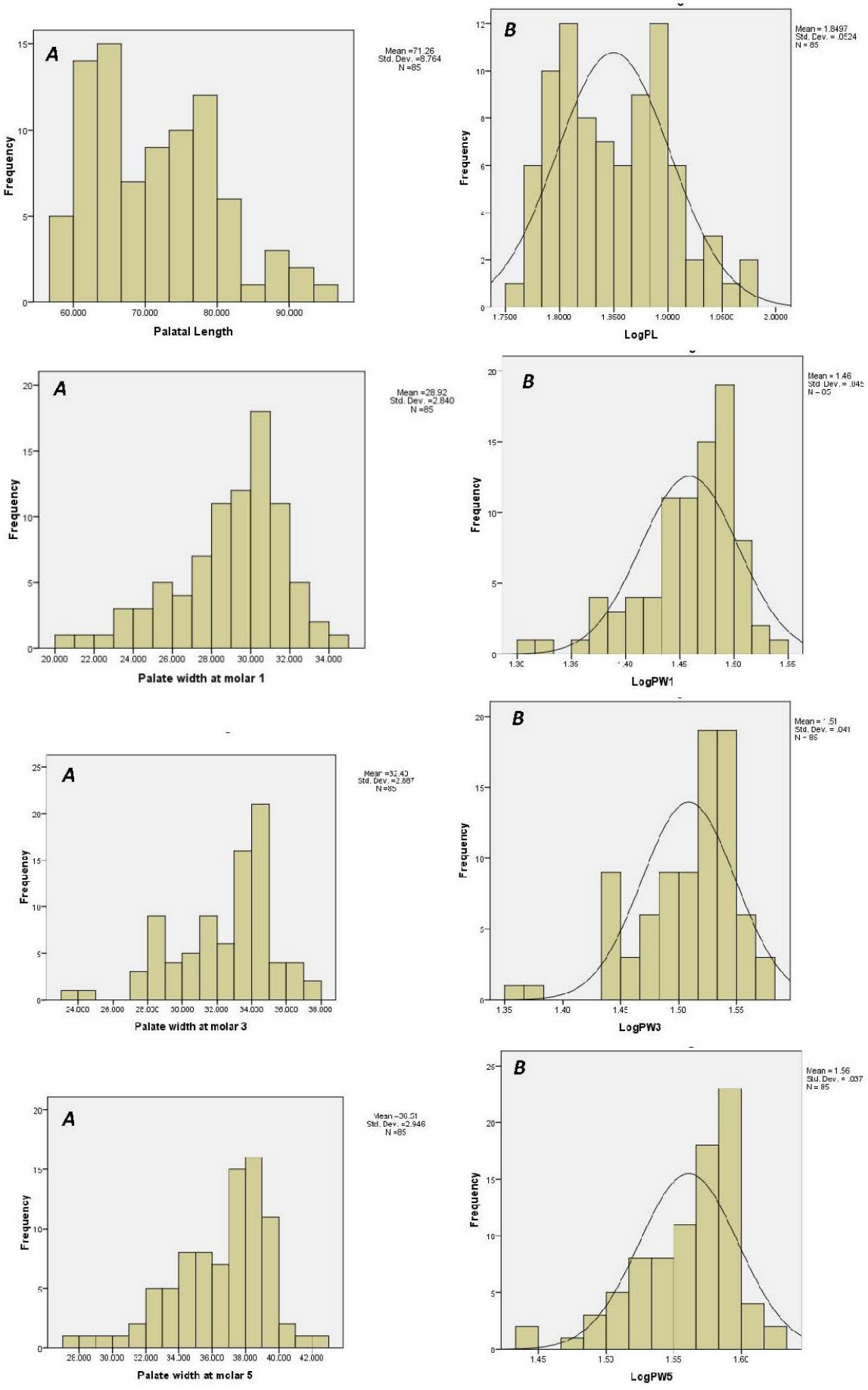


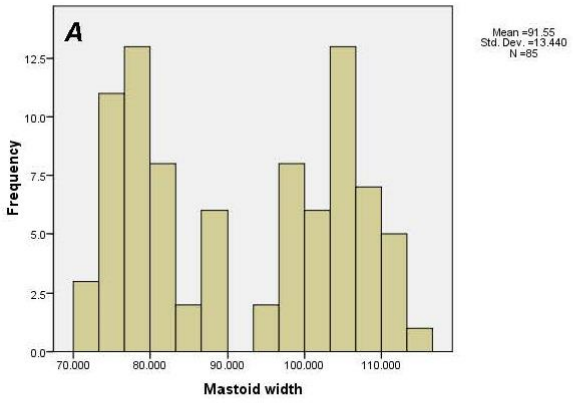
Fig: 4.8. A Principal Component Analysis (PCA) of all variables used in the discrimination of the Marion and Gough island populations' adult male Subantarctic fur seal skulls

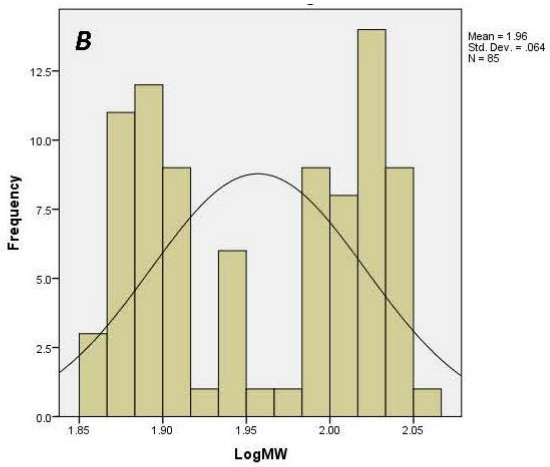
Table 4.3. The Discriminant Analysis (DA) results for the differentiation of the Marion and Gough island populations using all ten recorded variables.

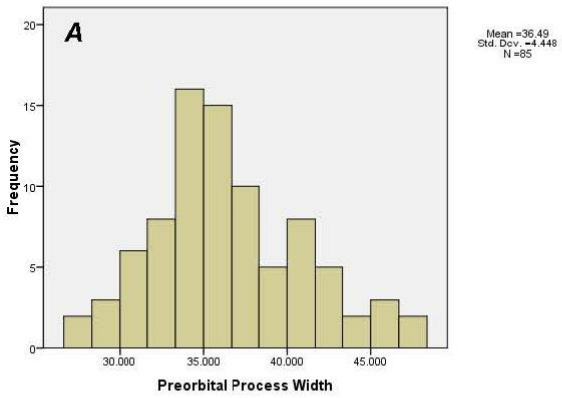
Standardized Canonical Discriminant Function Coefficients

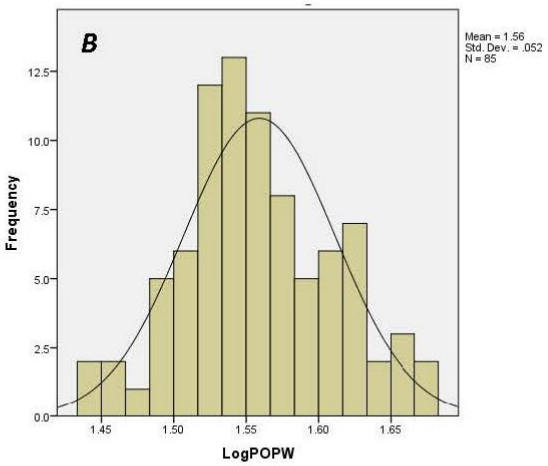
	Function 1
Palatal Length	.926
Palate width at molar 1	-.475
Palate width at molar 3	.218
Palate width at molar 5	-.753
Mastoid width	-.846
Preorbital Process Width	.720
Inter Orbital Process width	-.886
Skull Height	-.078
Upper Post canine Length	.828
Calvarial Root Width	.472

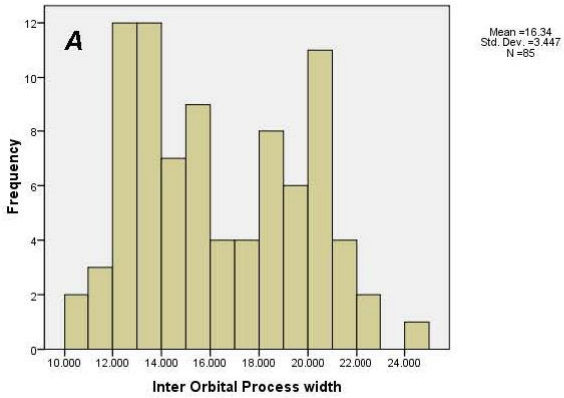

A
Mean =71.26
Std. Dev. =8.764
N =85
Frequency
Palatal Length
B
Mean = 1.8497
Std. Dev. = .0524
N = 85
Frequency
LogPL
A
Mean =28.92
Std. Dev. =2.840
N =85
Frequency
Palate width at molar 1
B
Mean = 1.46
Frequency
LogPW1
A
Mean =32.40
Std. Dev. =2.887
N =85
Frequency
Palate width at molar 3
B
Std. Dev. = .041
N = 85
Frequency
LogPW3
A
Frequency
Palate width at molar 5
B
Mean = 1.56
Std. Dev. = .037
N = 85
Frequency
LogPW5

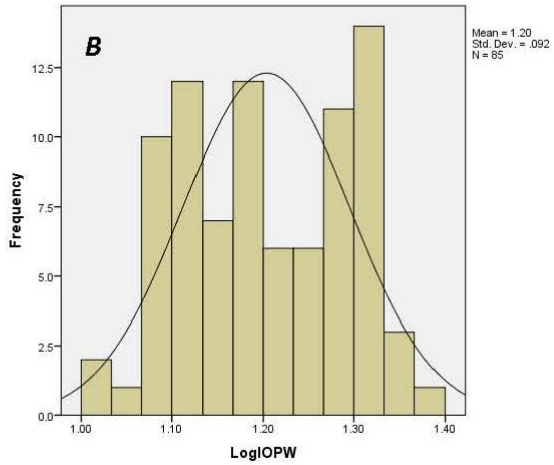

A
Mean =91.55
Std. Dev. =13.440
N =85
Frequency
Mastoid width


B
Mean = 1.96
Std. Dev. = .064
N = 85
Frequency
LogMW


A
Mean =36.49
Std. Dev. =4.448
N =85
Frequency
Preorbital Process Width


B
Mean = 1.56
Std. Dev. = .052
N = 85
Frequency
LogPOPW


A
Mean =16.34
Std. Dev. =3.447
N =85
Frequency
Inter Orbital Process width


B
Mean = 1.20
Std. Dev. = .092
N = 85
Frequency
LogIOPW

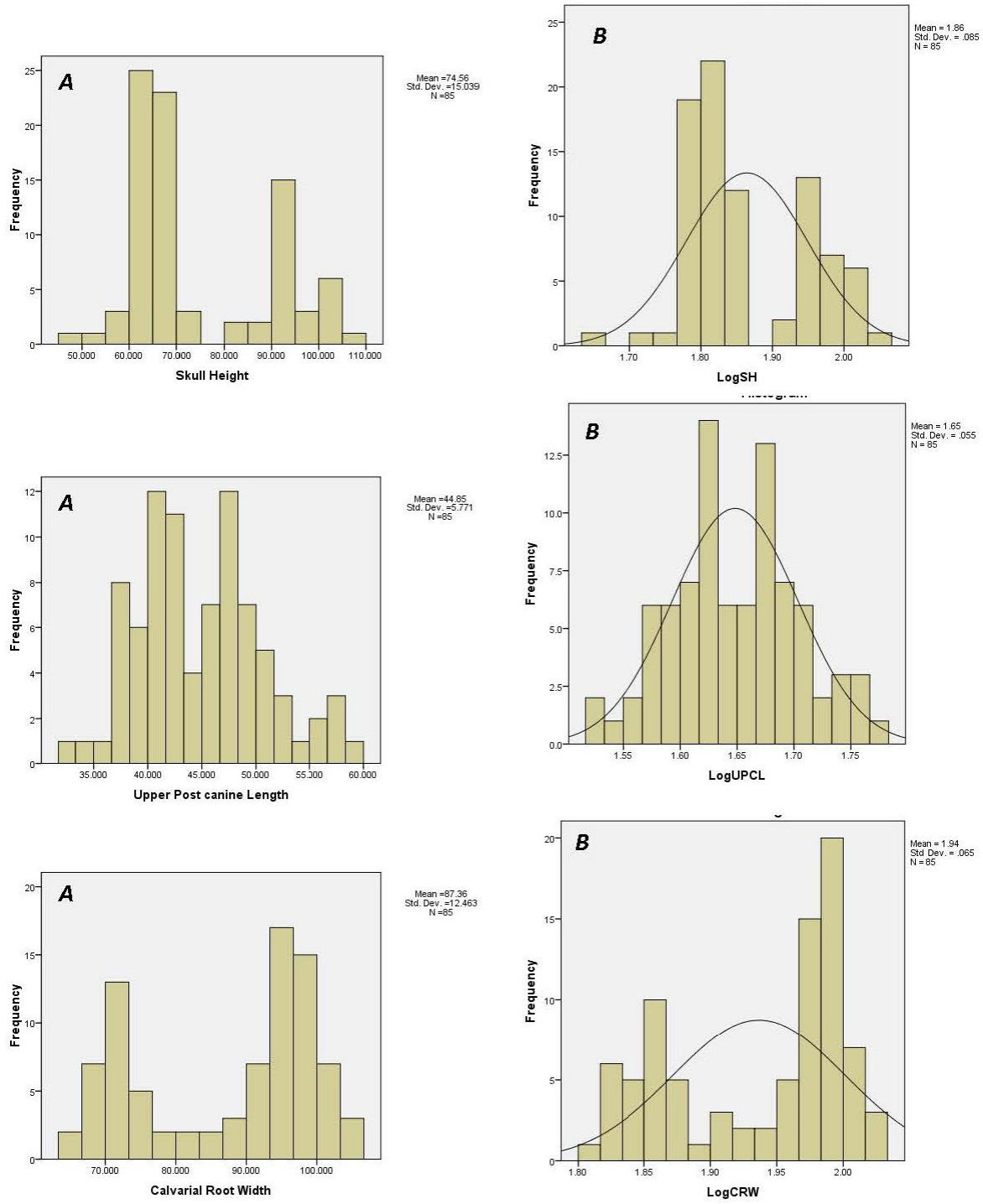
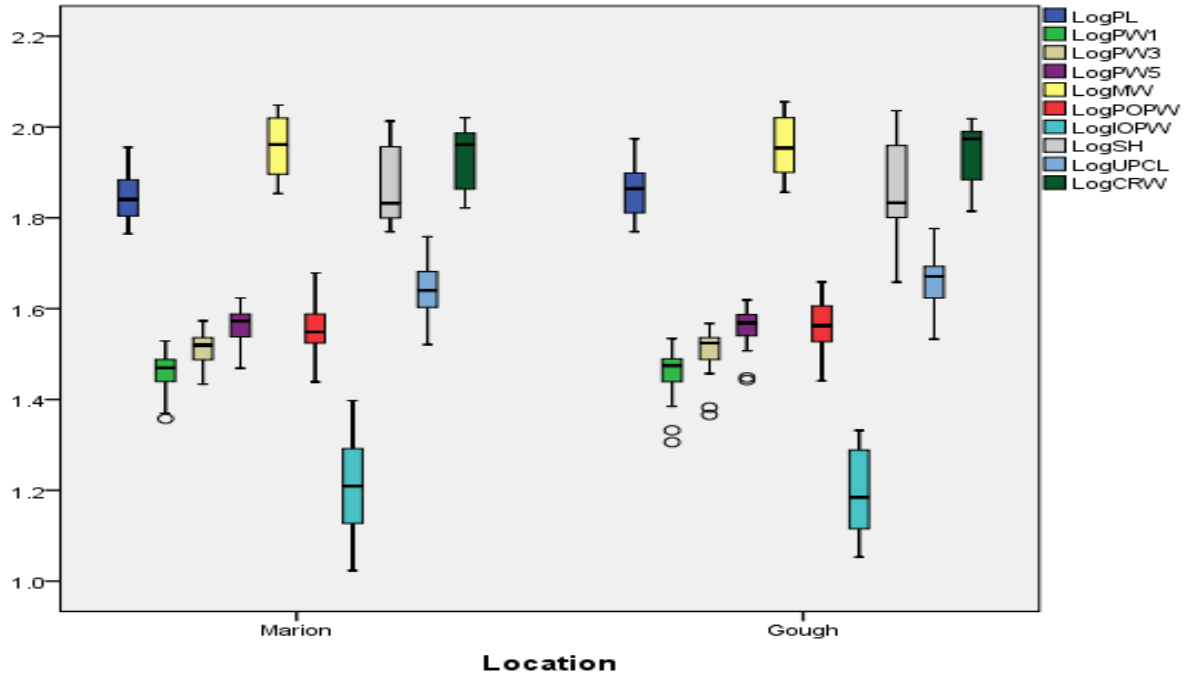


Fig 4.9. Histogram of all variables and data distribution of adult male skulls of Subantarctic fur seal between Marion Island and Gough Island populations, A, before transformation B, after natural Log transformation



Fig, 4.10. Stem and Leaf graph of skull morphometrics for all ten transformed variables from adult male skulls from the Marion Island and Gough Island populations.

The adult male Subantarctic fur seal of the Marion Island and Gough Island populations lie separated from each other (although not significantly different), the Gough Island population characterized by a slightly larger skull size in adult males (Fig 4.10), The SI means for Gough Island individuals (30.87) and Marion Island individuals (30.09) reflect that skulls of comparably aged animals were used, therefore strengthening the conclusions made from this study.

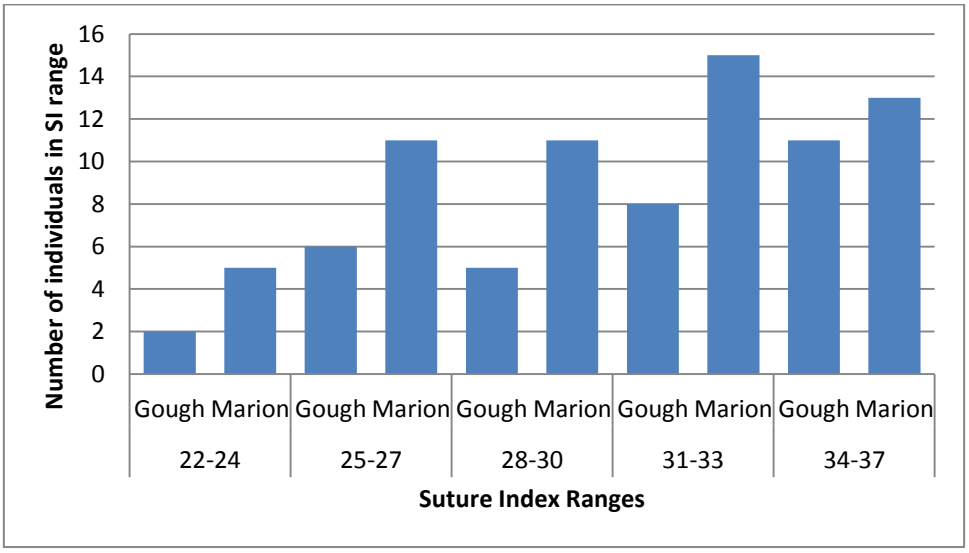


Fig 4.11. Suture Index (SI) of individual adult Subantarctic fur seal skulls considered for the analyses.

Discussion

The study found no significant difference in skull morphometrics of adult males between Gough Island and Marion Island populations. The results corroborate what has already been suggested by, for example, Kerley et al. (2000), Brunner (2002) and Stewardson et al. (2008). The differences in body size of *A. tropicalis* as reported by Bester and Van Jaarsveld (1994) might be attributed to seasonal abundance of food. The increased seasonal adult body size of Subantarctic fur seals might have little to no effect on skull size on a long term basis or the latitudinal difference is too little to show significant difference. The patterns of variation in some parameters such as palatal length, upper post canine length, and calvarial root have been described for these two populations (Kerley and Robinson 1987; Brunner 1998; Kerley et al. 2000; Brunner et al. 2002). The same patterns were observed in this study but reveal insignificant variation between the two populations counter to our initial expectations that these variables could reflect significant differences between the two populations. DA show that palatal length and upper post canine length have some degree of power in the skull metric variations.

One explanation for the absence of significant differences in skull measurements can be attributed to a low sample size, although measurements between the *A. gazella* from Marion Island and South Georgia Island revealed some degree of variation despite small sample size (Kerley and Robinson 1987). Bester and van Jaarsveld (1994) suggest that the two populations from Marion Island and Gough Island are subjected to varying environmental condition (Kerley and Robinson 1987; Kerley *et al.* 2002; this study). A further possible confounding factor to the comparison could be less accurate aging (SI) for the Marion Island individuals, as compared to the Gough samples (aged on GLG's from tooth sections) which is a more precise technique (Scheffer 1950; McCann 1993).

The historical events at these locations might account for the presence/ absence of differences in body size metrics between the two populations. The sealing practiced during the nineteenth century that resulted in dramatic decrease in seal populations throughout the Southern Ocean (Rand 1956; Bonner and Laws 1964; Shaughnessy 1976), might have reduced the variability between the two populations. However, the

decreased fecundity, increased mortality, and reduction in population growth resulting from reduced fitness (Caughley 1994) is not evident at Marion Island and Gough Island (Bester 1980; Kerley 1983; Hofmeyr et al. 1997).

Vagrant Subantarctic fur seals were recorded thousands of kilometres away from their native breeding grounds (Payne 1979; Goldsworthy and Shaughnessy 1989). Mostly lactating females travel in excess of 600 km (Bester 1990; Robinson et al. 2002; de Bruyn et al. 2009) away from their native breeding grounds during foraging trips. Hänel et al. (2005) recorded a subadult that had travelled 7000 km from its breeding ground at Amsterdam Island to Gough Island. There has also been several sightings of subadult vagrants at a variety of locations, e.g. South Georgia (Payne MR 1979), South Africa (Shaughnessy and Ross 1980), Angolan coast (Carr et al. 1985) the coast of Antarctica (Shaughnessy and Burton 1986); Brazil (Pinedo 1990); New Zealand (Taylor 1990); Australia (Gales et al. 1992); Comores (David and Salmon 2003); Madagascar (Garrigue and Ross 1996), Mauritius and Rodrigues (David and Salmon 2003); Bouvet Island (Hofmeyr et al. 2006); Zanzibar, Tanzania (Hofmeyr and Amir 2010), Gabon (Zanre and Bester 2011), and most recently at Livingston Island (Torres and Aguayo 1984). Bester (1981) proposed that rapid population increase accounts for the population instability at breeding grounds, resulting in high extralimital sightings. No recorded inter-island movement of fur seals between Marion and Gough islands exists (Condy 1978; Shaughnessy and Ross 1980; Bester 1984). However, the recorded capability of dispersal of *A. tropicalis* may suggest the opposite, such that inter-island migrations are likely to occur. This further makes the differentiation of the two populations complicated, as is the assessments of diagnostic skull morphological differences. Should inter-island migration occur, then this can explain the little variation in morphology between the two populations of Subantarctic fur seal which obviates the use of craniometrics to trace origins of vagrant Subantarctic fur seals (Kerley et al. 2000). However, a role of genetic drift in morphological differentiation cannot be disregarded. The observed great phenotypic variation in body size (Bester and Van Jaarsveld 1994) but no significant differences in skull craniometrics (Kerley et al. 2000) between geographically separate populations cannot not be explained in this study. Such questions can benefit from genetic studies.

The lack of detectable significant variation in *A. tropicalis* skull metrics between two populations from geographically distinct localities, suggests that Bergmann's Rule is not supported by the findings of this study. Other studies also suggest that *A. tropicalis* does not obey this rule (Stewardson et al. 2008), as do other animals such as minks (Stevens and Kennedy 2006), we also note that the species might be inhabiting areas that are not wide enough in latitudinal range.

Conclusion

In conclusion, this chapter has given an account of the application of 3D photogrammetry in interpopulation craniometrics of adult male Subantarctic fur seals. The present study confirms previous findings (Kerley and Robinson 1987, Kerley et al. 2002) and contributes additional evidence that suggests that there is no detectable skull variation between the Marion Island and Gough Island adult male Subantarctic fur seal population and that some skull variables (i.e., Palatal Length) show a pronounced degree of variation, although not statistically significant. Adult male Subantarctic fur seals do not conform to the Bergmann's rule as proposed by Brunner et al. (2000). The little variations observed in this study might have been influenced by historical factors, possibly interisland migration and interisland breeding. Based on our analysis, given the historical factors (Thorpe 1987) such as sealing and potential meta-population interbreeding and no detectable craniometric differences between the two populations from this study, it can therefore be speculated that skull morphometrics is not an adequate tool to discriminate the two populations. Small sample size might have compromised these conclusions. Further work needs to establish whether there exist interisland movement between the Marion Island and Gough Island populations and to characterise their genetic make-up.

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CHAPTER 5

General conclusion

Synthesis

The use of 3D models received intensive research attention in the last two decades (Alby et al. 2009), and this technique is a widely applied method in a variety of fields, ranging from biology, mining, filming, engineering, archaeology, industry, forensics, medicine, to architecture. This technique permits digital analysis of a given information set through a computer and software theoretically and algorithmically (Taşdemir et al. 2008) with greater accuracy (http://www.photomodeler.com). Alby et al. (2009) pointed out that, are major improvements in the performance of the existing digital solutions. Photogrammetry is a non-contact measurements technique (Luhmann et al. 2007) that allows you to convert the images of an object into a 3D model (Taşdemir et al. 2008). Digital close range photogrammetry is a technique used for accurately measuring objects directly from photographs or digital images captured with a camera at close range (Taşdemir et al. 2008).

There is a graded latitudinal difference in adult body size of Subantarctic fur seals *Arctocephalus tropicalis* (Bester and Van Jaarsveld 1994) but the skull morphometrics of adult males from two different populations were found to be similar (Kerley et al. 2000). There are many successful applications of close range photogrammetry, on a variety of fields and projects, yet none attempted to distinguish the two populations of Subantarctic fur seals at Marion and Gough islands. Using the latest morphometric technology (e.g. de Bruyn et al. 2009), I wanted to compare the adult male Subantarctic fur seal skull metrics within and between populations e.g., using craniometrics which allows accurate measurement (Kerley and Robinson 1987; Brunner 1998; Kerley et al. 2000; Stewardson et al. 2008)

Using carefully photographed images from skulls deposited at the Port Elizabeth Museum at Bayworld, and constructing detailed, high resolution 3D skull models, I attempt to assess the applicability of Photomodeler scanner® (PMSc®) in 3D skull model productions and in species and population differentiation.

Investigating the intraspecific and interspecific craniometrics of adult male Subantarctic fur seals and assessing the effectiveness of PMSc® in morphometric comparisons, it is imperative that the methodology be tested for applicability.

Hence Chapter 2 describes the step by step method of 3D skull modelling. Two Photomodeler® tools were tested, and were found to effectively produce 3D skull models. However, the Smartmatch® tool was the most effective for 3D modelling. The Smartmatch® tool produced more accurate and high resolution 3D skull models, within a shorter time compared to the Coded Target method and manual method. Therefore, PMSc® demonstrated a highly sensitive detection algorithm in the process of 3D modelling and is reliable and highly accurate method for 3D modelling.

In Chapter 3, I assessed the usefulness of photogrammetry through PMSc®, by accurately producing high resolution 3D skulls of adult male *A. tropicalis* and *A. gazella* that are separable through the traditional methods (Kerley and Robinson 1987). Using the 3D skulls models I compared eight cranial measurements between the two species which differed significantly and separated the two species unequivocally.

Lastly, in Chapter 4, using the acquired knowledge from both Chapter 2 and Chapter 3 alongside other published studies on photogrammetry. I investigated the usefulness of photogrammetry in craniometrics using PMSc®. I compared 3D skulls of *A. tropicalis* which are inseparable through traditional methods (Kerley et al. 2000). To determine whether there are any significant difference between different populations of *A. tropicalis*. All measured cranial variables did not show any significant difference between the two populations.

This study suggests that museum specimens can be accurately digitized and that digital museum collections can be created.

Further research

Further work needs to establish whether significant differences exist between the different populations of Subantarctic fur seals through increased sample sizes, perhaps looking into gender differences and age group specific studies. Future studies should incorporate genetic analyses, since craniometrics is regulated by genetic mechanisms (Manfredi et al. 1997; Johannsdottir et al. 2005). And assess the usefulness of PMSc® on cranial volumetric measurements to establish a holistic approach on assessing cranial differences.

This research will serve as a basis for future craniometrics studies. Taken together, these findings suggest an important role for Photogrammetry particularly PMSc® in Craniometry and other morphometric studies in different species. The methods used for this study may be applied to other morphometric studies elsewhere in the world and on any species. A number of possible future studies using the same experimental set up are apparent particularly in exploring/investigating other morphometric features.

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APPENDIX A

Calliper and 3D measurements of adult male *A. gazella* and *A. tropicalis*

This appendix includes the caliper and Photomodeler Scanner® (PMSc®) measurements. The caliper measurements were recorded from the actual specimens while the Photomodeler scanner measurements were recoded from the 3D replicas of the actual specimens.

Appendix A. Comparison of the cranial morphology of adult male Antarctic and Subantarctic fur seals recorded with a calliper and PMSc®, Port Elizabeth Museum (PEM), N refers to the species number.

Cranial Measurements		A= Calliper values								
Units mm		B=Photomodeler Values								
PEM Number	Condylobasal A	Condylobasal B	Supra Orbital A	Supra Orbital B	Braincase A	Braincase B	Palatal Length A	Palatal Length B	Ventral width A	Ventral width B
N3915	222.12	221.970	40.62	40.55	56.81	57.03	82.73	82.59	27.29	27.44
N3913	222.94	223.070	49.74	49.417	58.03	57.915	74.9	75.01	29.26	28.976
N3918	223.9	223.870	42.39	42.27	54.03	53.874	79.96	80.196	23.55	24.067
N3914	218.97	219.110	48.41	48.601	60.21	60.09	72.97	72.84	19.46	18.97
N4255	228.8	229.062	44.92	45.171	58.37	58.458	71.13	71.242	26.97	27.055
N4256	223.95	224.070	38.48	38.67	55.49	55.73	82.23	81.83	18.64	18.38
N4259	227.72	227.320	52.07	52.12	59.57	59.613	76.04	76.13	21.46	21.615
N4260	206.55	207.183	45.13	44.93	52.59	52.33	68.24	68.11	19.21	19.128
N4290	237.61	237.389	59.26	59.14	59.96	60.01	90.2	89.91	33.94	33.698
N4297	227.49	228.129	48.11	48.33	51.61	51.945	76.59	77.075	36.27	36.24
N4300	215.28	215.490	48.13	48.21	57.85	56.791	78.69	79.049	33.92	33.739
N4298	230.92	231.020	54.41	54.37	61.48	61.44	80.89	81.038	37.39	37.11
N4299	240.45	239.688	55.98	56.03	53.93	54.231	83.32	82.898	38.36	38.23
N4304	225.23	225.115	64.44	64.53	64.62	65.035	88.44	88.271	36.29	36.687
N4305	227.12	228.075	69.51	69.23	58.83	59.017	82.52	82.845	36.25	36.52
N4306	224.31	223.933	52.28	52.33	53.14	53.26	76.64	77.059	33.03	32.931