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Water column usage and environmental determinants in southern elephant seals from Marion Island

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Submitted in fulfilment of the requirements of
Doctor of Philosophy (Zoology)

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July 2011

Declaration:

I, Trevor McIntyre, declare that the thesis/dissertation, which I hereby submit for the degree PhD 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:………………………………………..

WATER COLUMN USAGE AND ENVIRONMENTAL DETERMINANTS IN SOUTHERN ELEPHANT SEALS FROM MARION ISLAND

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Abstract

Southern elephant seals (*Mirounga leonina*) are relatively common top predators and major consumers within the Southern Ocean. This study aimed to describe the at-sea behaviour of a small population of southern elephant seals at Marion Island and to place this behaviour into an ecological and evolutionary context. Calculations of life-time habitat use for animals from this population revealed that seals spent an average of 77.59% of their lives diving at sea, 7.06% at the sea surface, and 15.35% hauled out on land. Animals from this population evidently tended to dive deeper than reported for other populations. Their extreme dive behaviour, and apparent shorter reproductive lifespans than animals from some other populations led to a 'deeper diving – shorter life' hypothesis, suggesting that Marion Island elephant seals may carry substantial physiological costs associated with deeper diving.

Mean dive depths (± SD) recorded for female seals were 560 ± 170 m during the day and 394 ± 153 m at night. Male seals dived to a mean depth of 618 ± 259 m during the day and 480 ± 272 m at night. Female seals mostly foraged pelagically on vertically migrating prey, displaying positive diel vertical migration in their dive depths. Individual variation existed though, and some females tended to display a reverse pattern of diving deeper at night, compared to daytime dives. Adult male seals displayed more individual variation in forage strategies, though the majority still favoured foraging pelagically, and not benthically as described for other populations. Subadult males tended to use dive strategies that always resulted in dive patterns that exhibited diel variation in dive depths. By implementing a refined method that combines dive type analyses with relative amounts of time spent at the bottom of forage dives, descriptions are provided of the spatial areas of increased forage effort for male and female seals. Female seals tended to concentrate their forage efforts in areas further away from the island, rarely displaying forage effort dives within a radius of ~ 250 km from Marion Island. Adult males concentrated their forage effort dives in areas in closer proximity to the island, while subadult males displayed more variation and often foraged at similar distances from the island and within similar areas as adult females. These results suggest that subadult males and adult females are more reliant on vertically migrating prey in pelagic environments than adult males from the same population. Nevertheless, competition for food resources between subadult males and adult females appears unlikely, since subadult males target deeper water layers than adult females.

Due to the extreme sexual size dimorphism exhibited by southern elephant seals, it is unclear whether observed differences in dive behaviour are due to increased physiological capacity of males (when compared to females) or differences in activity budgets and foraging behaviour. By making use of mixed-effects models on dive results obtained from a sample of similarly-sized male and female elephant seals, I investigated the comparative influences of sex, body size and age on measured dive parameters. Model outputs indicated that, while individual variation accounted for substantial portions of total model variance for many response variables, differences in maximum- and targeted dive depths were always influenced by sex, and only partly by body length (used as a proxy for body size). Conversely, dive durations were always influenced by body length, while sex was not identified as a significant influence. These results support hypotheses that dive durations of elephant seals are limited by physiological capacity associated with body size. However, the influence of sex on the depths dived to indicate differences in forage selection between sexes in this species and possible avoidance of inter-sexual competition.

Further investigations into the influences of various environmental variables (bathymetry, temperature at depth, T_{max} below 100m) as well as demographic and behavioural variables (migration stage, age-class, track day and vertical diel strategy) on dive behaviour indicated a consistent association between dive depths and *in situ* water temperature. While much individual variation was apparent and other variables also played significant roles, animals consistently dived deeper, and spent less time at targeted depths, when diving in warmer water masses. This is most likely explained by differences in suitable prey distributions at different temperatures. Predicted climate change in the Southern Ocean suggests an overall continued warming, resulting in elephant seals from Marion Island likely having to dive to deeper depths in search of suitable prey and/or shift their migration routes poleward. This may have negative consequence for this population, since animals from Marion Island are presumably already operating closer to their physiological limit compared to other populations.

Key words: southern elephant seals; Marion Island; dive behaviour; forage strategy; satellite-relay data logger; sexual segregation; climate change; foraging ecology

ACKNOWLEDGEMENTS

This project was financially and logistically supported by the South African National Antarctic Programme, the South African Department of Science and Technology through the National Research Foundation, the University of Pretoria and the Alfred Wegener Institute for Polar and Marine Research. Much of the data was collected under the auspices of Marine Mammals Exploring the Oceans Pole to Pole (MEOP), a multi-national International Polar Year (IPY) initiative.

I wish to thank all the people involved with the collection of data associated with the ongoing long-term mark-recapture experiment on Marion Island. In particular, the following people assisted with the deployments of satellite-relay data loggers between 2004 and 2008: Greg Hofmeyr; Dr. Brent Stewart, Phathu Radzilani; Dr. Nico de Bruyn, Dr. Cheryl Tosh, Chris Oosthuizen, Mashudu Phalanndwa; Ryan Reisinger and Thomas Mufanadzo. Dr. Nico de Bruyn and Dr. Cheryl Tosh are also further thanked for their valuable input into many facets of this project.

A very big thank you to Prof. Marthán Bester for providing me with all the fantastic opportunities associated with overwintering on Marion Island and the ensuing research project. Your optimism, support and guidance are greatly appreciated! Thank you also to Dr. Isabelle Ansorge, my co-promoter, for your enthusiasm toward this project, your support and willingness to get involved with data not always emanating from a ship.

Our collaborators at the Alfred Wegener Institute, Dr. Joachim Plötz and Dr. Horst Bornemann, are thanked for their support of this project and for providing me with memorable field experiences, and great opportunities to get involved in various aspects of seal research. Dr. Martin Biuw is gratefully acknowledged for freely sharing his insights and allowing me to pick his brain.

I would also like to thank my family and particularly my parents for their unconditional support throughout. You've provided me with the stable and supportive environment to develop and follow my own dreams. Then I wish to also thank Natalie Haussmann for her love, companionship, support and motivation throughout. Being able to laugh with you at the end of sometimes difficult days definitely made things a lot easier! Various friends, colleagues, teachers and mentors (both present and past, and certainly too many to list!) are also thanked for each imparting his/her own positive influence and contribution.

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Disclaimer

Each of the research chapters in this thesis was structured with its publication in a scientific journal in mind. I therefore apologise for some inevitable overlap and repetition in methods sections. Where chapters have been published or are under review, the publication details are included in the first page of the chapter as a footnote. While each chapter benefitted from the input of various co-authors, I undertook all analyses pertaining to the water column use of elephant seals and wrote the chapters.

CHAPTER ONE: GENERAL INTRODUCTION

Southern elephant seal background

Elephant seals are the largest members of the family Phocidae. Two species are recognised, namely southern- (*Mirounga leonina*) (Linnaeus 1758) and northern (*M. angustirostris*) (Gill 1866) elephant seals. The origins of the genus and the relationship between the species are obscure and opinions vary regarding their evolutionary history (Le Boeuf & Laws 1994a), though there appears to be some agreement about their relationship to other members of the Monachinae (Arnason et al. 2006; Higdon et al. 2007). Southern elephant seals are the larger of the two species (King 1983) and display extreme sexual dimorphism – males sometimes weighing in excess of 3 500 kg, while females weigh on average between 400 kg and 600 kg (Laws 1953).

Southern elephant seals have a circumpolar distribution and breeding colonies are established on a number of subantarctic islands, as well as mainland sites on the South American continent and Antarctica (Laws 1994). Four genetically distinct sub-populations have been identified, namely the Peninsula Valdés (Argentina), South Georgia, Kerguelen and Macquarie stocks (Slade et al. 1998). The South Georgia population is the largest of all populations and together with the populations at Peninsula Valdés, Heard-, Macquarie- and Kerguelen Islands comprise up to 98% of the global stock of southern elephant seals (de Bruyn 2009). The remaining populations are scattered throughout the subantarctic on various islands, including Bouvetoya and the Prince Edward Islands. Elephant seals spend the majority of their time on protracted migrations at sea and generally return to land twice a year, once for the breeding haulout and once for the obligatory moult (Le Boeuf & Laws 1994b). A third haulout is sometimes undertaken by immature animals, particularly males during winter months (Kirkman et al. 2001). This winter haulout is poorly understood and its role in elephant seals’ life history uncertain.

During their foraging migrations, southern elephant seals often travel great distances in search of prey. Such distances are known to vary between individuals and between migration stages – post-breeding migrations generally being shorter than post-moult migrations. While at sea, elephant seals are known to be extreme divers, spending the majority of their time below the sea surface (Hindell et al. 1991). Dives are often deeper than 1 000 m, and can last for periods longer than 90 min (Bennet et al. 2001). Diving marine mammals exhibit various adaptations to increase the amount of time that they can spend underwater – such adaptations include: elevated concentrations of haeomo- and myglobin (Ridgway & Johnston 1966; Polasek & Davis 2001); lung collapse (Falke et al. 1985); compressible tracheas (Bostrom et al. 2008); reductions in metabolic rates and cardiac outputs (Kooyman & Ponganis 1998; Fahlman et al. 2006); as well as increased resistance to hypoxia in neuronal tissues (Folkow et al. 2008; Mitz et al. 2009). Such adaptations are likely present in elephant seals, given the extreme diving behaviour that has been recorded for this group. Recently, Meir et al (Meir et al. 2009) further demonstrated the capability of northern elephant seals to exhaust blood oxygen levels and thereby maximise their aerobic dive durations.

Southern elephant seals at Marion Island

The Southern Ocean is characterised by its conspicuous frontal banding patterns (Belkin & Gordon 1996). The positions of these fronts display a highly dynamic pattern, with variations in their positions of up to 100 km in 10 days having been observed (Carmack 1990). Marion Island (46°54'S; 37°45'E) is the larger of two islands collectively forming the Prince Edward Islands (PEI). These islands are situated within the Polar Frontal Zone (PFZ) of the Southern Ocean, the Subantarctic Front (SAF) being situated directly to the north of the islands and the Antarctic Polar Front (APF) situated to the south of the islands (Lutjeharms & Ansorge 2006). Major bathymetric features in the vicinity of the islands include the South-West Indian Ridge (SWIR), the Del Cano Rise (DCR), the Conrad Rise (CR) and the Crozet Plateau (CP) (Fig. 1.1). The Antarctic Circumpolar Current (ACC) forms the dominant background current influencing the PEI region, and flows in an eastward direction. Regions of high mesoscale variability occur in the vicinity of the PEI, mainly as a result of a dynamic population of eddies of different sizes and circulation directions that characterise the area (Ansorge & Lutjeharms 2002; Ansorge & Lutjeharms 2003). Whilst a number of hydrographic surveys have been undertaken in the vicinity of the PEI, comparatively few areas have been studied in detail, notable exceptions being the shelf area between Marion- and Prince Edward Island and the region surrounding the SWIR (Ansorge & Lutjeharms 2002).

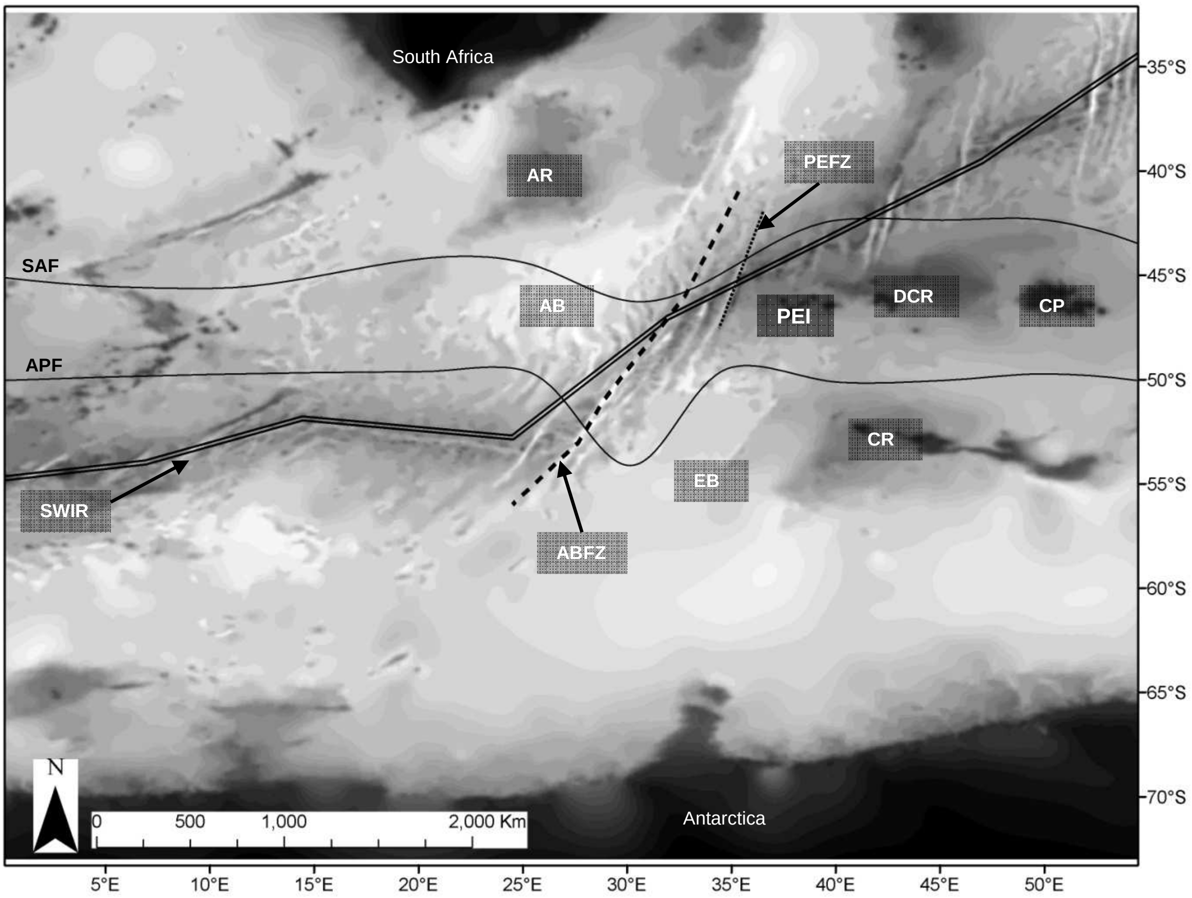

Figure 1.1: Oceanographic and bathymetric setting of the Prince Edward Islands (PEI). Major bathymetric features in the surrounding areas include the South-West Indian Ridge (SWIR), Andrew Bain Fracture Zone (ABFZ), Prince Edward Fracture Zone (PEFZ), Agulhas Rise (AR), Agulhas Basin (AB), Enderby Basin (EB), Del Cano Rise (DCR), Conrad Rise (CR) and Crozet Plateau (CP). Approximate positions of the Subantarctic Front (SAF) and Antarctic Polar Front (APF) follow Belkin & Gordon (1996).

The long-term mark-resighting research programme of southern elephant seals on Marion Island (Bester 1988b) has resulted in various insights into the population dynamics and status of southern elephant seals in the Southern Ocean. The elephant seal population at Marion Island showed a dramatic decline of approximately 83% between the 1950s and 1990 (Laws 1994). While population numbers have stabilised and even slightly increased since 1990 (de Bruyn 2009), the exact mechanisms explaining the decline are not well understood (Pistorius et al. 1999; 2004; McMahon et al. 2005; 2008). The extensive nature of the mark-resighting programme enables researchers to determine the origins, ages, haul-out histories and reproductive success of many individual animals on the island. This information has been used to select appropriate animals for the deployments of tracking devices (e.g. animals likely to return to Marion Island etc.). It further allows for multiple, sequential deployments of devices on the same animals in order to investigate temporal variation in foraging locations and dive behaviour in relation to reproductive success and fitness.

Technological advances in animal-borne instruments

The use of animal-borne instruments to record aspects of the behaviour of marine animals dates back as far as the 1940s when simple maximum depth recorders were developed (Scholander 1940). Kooyman and co-authors (Kooyman 1965; Kooyman et al. 1976) developed some of the first elementary time-depth recording devices, allowing researchers some valuable and first insights into the depths reached by Weddell seals (*Leptonychotes weddellii*) and northern fur seals (*Callorhinus ursinus*) during their dives and basic behaviour. Developments were also made independently from the early 1980s by Japanese researchers, largely under the guidance of Naito (Naito 2010) and starting with simple animal-borne recorders and mechanical time-depth recorders. Many advances have since been made in miniaturisation, battery capacities and digital capabilities. Latest technologies incorporate accelerometers allowing for detailed reconstructions of dive profiles and the inferring of detailed behavioural states (Mitani et al. 2004; 2009; Naito et al. 2010). The development of still- and video imaging technologies as part of animal-borne instruments is also advancing and shows much promise for elucidating animal behaviour in previously unexplored detail (Watanabe et al. 2006; Moll et al. 2007; Sakamoto et al. 2009).

Various devices have been manufactured in order to obtain track information from migrating marine mammals. Some of the earliest such devices relied on estimates of sea surface light levels and times of dawn and dusk (geolocation) to calculate approximate global positions (Hill 1994). Satellite-linked tags in turn have largely relied on position estimates obtained through Doppler shift calculations via Service Argos (Argos 1996) for increased accuracy. Lately satellite-linked devices that incorporate fast-loc GPS technology have led to even better location accuracies being obtained for various tracked marine animals (Witt et al. 2010).

Satellite-relay data loggers (Sea Mammal Research Unit, University of St. Andrews) have been in development since the 1980's (Fedak 2004). The Series 9000 SRDL provides information on the dive behaviour (time-depth profiles) of tagged animals, as well as temperature profiles recorded during dives. These devices consist of a microprocessor, D-cell battery, pressure transducer, antennae and temperature probe embedded in a solid resin pressure tested to depths of up to 2 000 m. Due to bandwidth restriction on the Argos system, micro-processors onboard the SRDLs provide abstracted time-depth and temperature profiles for transmission. Time-depth profiles therefore consist of the deepest point of each dive, as well as three other depth points (each with an associated time value) abstracted from the full profile using a broken-stick algorithm (Fedak et al. 2001). Temperature profiles normally consist of temperatures recorded at a number of pre-defined depths, as well as additional temperature points also abstracted using a broken-stick method. Temperature profiles are considered to have an accuracy better than 0.01° C (Boehme et al. 2009). Following the Series 9000 SRDL, CTD-SRDLs were developed, based on the Series 9000 model, but additionally incorporating an inductive cell (Valeport Ltd.), capable of measuring conductivity to an accuracy of approximately 0.01 mS/cm and resulting in salinity estimates with an accuracy of approximately 0.02 (Boehme et al. 2009) (Fig. 1.2). Recently, fluorescence sensors were also incorporated into the CTD-SRDL design, allowing recordings of chlorophyll concentrations along dive profiles of instrumented animals (Charrassin et al. 2009).

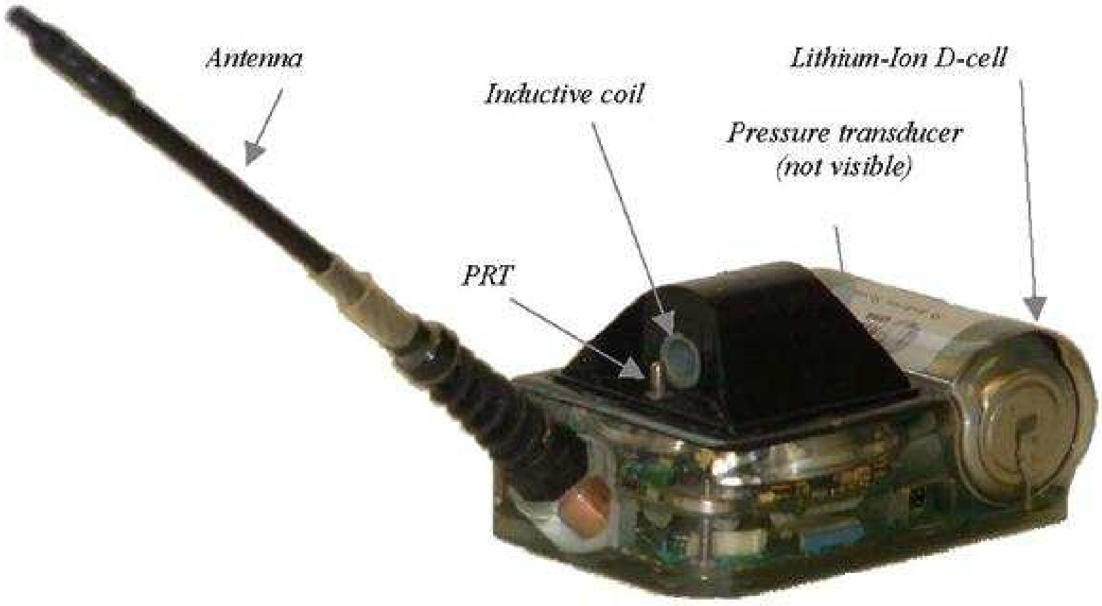

Figure 1.2: Image of Conductivity-Temperature-Depth Satellite-Relay Data Logger (CTD-SRDL) indicating the location of various components. PRT = platinum resistance temperature detector. Image obtained from http://www.smru.st-andrews.ac.uk.

A number of elephant seal movement studies have been conducted on animals from Marion Island. Such studies were initially at a relatively broad scale and showed that female animals utilize areas along the major frontal zones such as the APF and the SAF (Bester & Pansegrouw 1992; Jonker & Bester 1998). Additionally, the interfrontal zones between the Subtropical Convergence (STC) and SAF were considered likely to be of particular importance to post-breeding female seals (Jonker & Bester 1998). Adult male seals from Marion Island tended to remain closer to the island, foraging mostly pelagically (Malherbe 1998). Finer-scale investigations were carried out recently to investigate the associations of Marion Island elephant seal movements with oceanographic features also at a mesoscale (eddies, meanders etc.) (Tosh 2010). Results from this study showed that various oceanographic factors such as sea-surface temperatures, chlorophyll concentrations and sea-surface height anomalies evidently influenced seal movements. Movement patterns were more predictable for juvenile animals which evidently relied on displayed movement patterns linked to surface oceanographic variables. Much individual variation in movement patterns was evident though, particularly for adult male seals. While these results provided detailed overviews of elephant seal movements and how these relate to oceanographic features, no underwater behaviour was explored.

Aims

Southern elephant seals from Marion Island are exposed to different oceanographic environments compared to other large populations located further south. Their distance from continental shelves and the sea ice zone result in animals having to utilise very deep waters for foraging purposes or having to travel great distances to make use of areas with shallower bathymetry. This study aimed to investigate the underwater habitat use of Marion Island southern elephant seals in relation to environmental variables. I used data obtained from the deployment of SRDLs (Series 9000 and CTD-SRDLs) on Marion Island elephant seals between 2004 and 2008 and had the following specific aims:

- To quantify the lifetime habitat use of Marion Island southern elephant seals and elaborate on the potential consequences thereof on their life history (Chapter 2);
- To develop a suitable measure of forage effort and forage strategy in elephant seals that can be used to describe the water column use of elephant seals spatially (Chapters 3 and 4);
- To describe and compare the water column use patterns of elephant seals by sex, age class and migration stage (Chapters 3 and 4);
- To apply suitable statistical models to identify the main drivers in the behaviour and water column use of elephant seals (Chapters 5 and 6);
- To investigate the underlying causes of differences observed in water column use between male and female elephant seals (Chapter 5);
- To investigate the influence of oceanographic conditions on the water column use of Marion Island elephant seals, particularly within the context of predicted future climate changes (Chapter 6).

Thesis structure

This thesis is structured into 7 chapters. Chapter 1 is a general introduction providing relevant background information regarding southern elephant seals, the Marion Island elephant seal population, animal-borne instrumentation and the aims of this project. In chapter 2 I assess the lifetime habitat use of southern elephant seals at Marion Island by calculating actual amounts of time that animals spend in various environments. Chapter 3 and 4 describes the water column usages of female and male southern elephant seals in more detail. Here I provide descriptions of where animals increased their forage efforts and employed various dive strategies in a spatial framework. Chapter 5 explores the drivers behind evident sexual segregation in depths use patterns by southern elephant seals. The relationship of diving parameters with the *in situ* environments that animals dive in is explored in chapter 6. The results from this chapter present some important potential implications for the future at-sea behaviour of elephant seals from Marion Island under current climate predictions. Finally, chapter 7 provides a conclusion to the thesis, providing brief overviews of the implications of the results found in the thesis, shortcomings in our current understanding and suggestions for future research.

CHAPTER TWO: A LIFETIME AT DEPTH: VERTICAL DISTRIBUTION OF SOUTHERN ELEPHANT SEALS IN THE WATER COLUMN*

Abstract

Although numerous studies have addressed the migration and dive behaviour of southern elephant seals (*Mirounga leonina*), questions remain about their habitat use in the marine environment. We report on the vertical use of the water column in the species and the potential lifetime implications for southern elephant seals from Marion Island. Long-term mark-resight data were used to complement vertical habitat use for 35 known individuals tagged with satellite-relay data loggers, resulting in cumulative depth use extrapolated for each individual over its estimated lifespan. Seals spent on average 77.59% of their lives diving at sea, 7.06% at the sea surface, and 15.35% hauled out on land. Some segregation was observed in maximum dive depths and depth use between male and female animals – males evidently being physiologically more capable of exploiting increased depths. Females and males spent 86.98% and 80.89% of their lives at sea respectively. While at sea, all animals spent more time between 300m and 400m depth, than any other depth category. Males and females spent comparable percentages of their lifetimes below 100 m depth (males: 65.54%; females: 68.92%), though males spent 8.98% of their lives at depths in excess of 700 m, compared to females' 1.84% at such depths. Adult males often performed benthic dives in excess of 2 000 m, including the deepest known recorded dive of any air-breathing vertebrate (> 2 133 m). Our results provide a close approximation of vertical habitat use by southern elephant seals, extrapolated over their life spans, and we discuss some physiological and developmental implications of their variable depth use.

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* Published as: McIntyre, T., de Bruyn, P.J.N., Ansorge, I.J., Bester, M.N., Bornemann, H., Plötz, J. & Tosh, C.A. 2010. A lifetime at depth: vertical distribution of southern elephant seals in the water column. *Polar Biology* 33 1037-1048.

Introduction

Elephant seals (*Mirounga* spp.) are amongst the most intensively studied marine mammals and much is known about their behaviour, physiology and population dynamics as a result of their ubiquitous terrestrial phase (Le Boeuf & Laws 1994b). In recent years, advances in technology and reduced instrument sizes have allowed researchers to deploy a variety of devices on these animals, in order to gain some insights into their migrations and behaviour at sea (Bornemann et al. 2000; Biuw et al. 2007; Zeno et al. 2008; Tosh et al. 2009). Despite these advances, many questions remain about the characteristics of underwater areas targeted by elephant seals, diets of the seals and adaptations to deep diving (Hindell et al. 1992; Kooyman 2006). A fundamental gap in our understanding of elephant seal dive behaviour is whether the data collected via satellite over a short time period is representative of the conditions that elephant seals are exposed to over their lifetimes.

Diving behaviour of southern elephant seals has been described at numerous localities (Hindell et al. 1991; McConnell et al. 1992; Jonker & Bester 1994; McConnell & Fedak 1996; Campagna et al. 1999; Bornemann et al. 2000; Bradshaw et al. 2004; Bailleul et al. 2007a; 2008). Data from these investigations have shown that elephant seals spend up to 90% of their time at sea diving with dives lasting on average between 20 and 30 min, resulting in surface intervals of approximately two to three minutes (Hindell et al. 1991). Although the diving behaviour of southern elephant seals from different populations appears to be similar, some variation has been reported between populations, sexes and age-classes. Adult females from Macquarie Island displayed mainly pelagic diving behaviour, while males performed benthic, as well as pelagic dives (Hindell et al. 1991). One of four female elephant seals on South Georgia fitted with satellite-linked data loggers demonstrated many dives to the seabed, implying benthic feeding (McConnell et al. 1992). Southern elephant seals from Peninsula Valdés have shown marked variability in migrations and depth use between sexes and age-classes. Adult females appeared to concentrate foraging activity in pelagic, deep water (Campagna et al. 1995), whilst adult males performed benthic dives in relatively shallow water and pelagic dives over deeper waters (Campagna et al. 1999). Juveniles from the same locality, however, appeared to spend substantial amounts of time foraging on the Patagonian shelf, with females foraging closer to the shelf break than males that tended to use mid-shelf waters (Campagna et al. 2007). Male elephant seals from Marion Island displayed much variability in dive depths and dive duration (Malherbe 1998), whilst females displayed more consistent dive depths and durations, targeting pelagic prey (Jonker & Bester 1994).

Many of these investigations have relied on data from relatively few satellite-tracked animals (n = 4-13) that were mostly not previously known to the researchers (i.e. of unknown age and origin) and not subject to further investigations that would allow assessments of post-deployment survival, breeding success and growth. In this study a comprehensive mark-resighting dataset for the Marion Island elephant seal population allowed us to deploy satellite-relay data loggers on known individuals, born on the island and resighted in subsequent years. Dive data were then used, in conjunction with individual haulout histories and patterns, to quantify the amounts of time spent by southern elephant seals in different environments over an extended temporal scale. We use this information to construct an understanding of lifetime habitat use in this species, as opposed to the hitherto collected short-term deployment/depth-use data, and discuss some physiological and demographic implications of this lifetime habitat use.

Methods

Satellite tagging

Since 2004, a total of 59 satellite-relay data loggers (Sea Mammal Research Institute, University of St. Andrews, Scotland) were deployed on southern elephant seals hauled out at Marion Island (46°54'S; 37°45'E). Two types of satellite-relay data logger (SRDL) were used for these deployments. Thirty-five SMRU series 9000 SRDLs, capable of measuring pressure and temperature were deployed, followed by 24 CTD-SRDLs, capable of additionally measuring conductivity. Devices were deployed on 28 adult females (older than 3 years), 4 subadult females (2-3 years old), 9 adult males (older than 6 years), 16 subadult males (2-6 years old), 1 yearling male (1-2 years old) and 1 under-yearling male (0-1 year old). All animals were immobilised using a remote injection method to inject calculated dosages of ketamine (Bester 1988a). Following immobilisation, SRDLs were glued to the fur on the heads of study animals using quick-setting epoxy resin (Araldite®, Ciba Geigy).

Dive data

The SRDLs were configured to measure depth points every four seconds during dives (dives were defined as starting below 6 m depth). Upon detection of the end of each dive, data loggers calculated the four internal points in each profile that gave the best fit to each profile. This allowed for substantial compression of the dive data and more reliable transmission rates over the Argos satellite system. Since southern elephant seals undertake prolonged migrations that can last longer than eight months, such compression of data is important to maximise battery life of the SRDLs. Data were then stored temporarily in a buffer by the device, and profiles were randomly transmitted from the buffer to ensure individual dive profiles have equal chances of being received and relayed by the Argos system. All dive data and related meta-information are available via the PANGAEA information system (www.pangaea.de). Estimates of the ocean bottom depth were obtained for each dive location (Smith & Sandwell 1997), allowing for estimates of relative depth of each dive (pelagic vs. benthic).

Dive analyses

Prior to analysis, all dive data were filtered to remove incomplete dive sequences or unrealistic dive point sequences. The unrealistic dive point sequences were those that contained errors in time-value sequences, but were comparatively few (ca. 1 dive per 5 000 recorded dives). Errors in dive sequences are largely the results of interruptions to uplinks with the Argos satellite during surfacing events of the seals. Diving data obtained from the SRDLs consist of four maximum inflection points, calculated prior to transmission onboard the device by a broken-stick algorithm (Fedak et al. 2001). These four points include the maximum dive depth reached during each dive, as well as the percentage of dive duration passed at each point. The information obtained in such a way can be used to infer the general dive-shape and other behavioural characteristics of each dive (Biuw et al. 2003). Because differences in dive depth between individual points can be large (often in excess of 500 m), it is difficult to get finer-scale information about the amount of time the animal spent at specific depths. We therefore developed a calculation to estimate the amount of time spent within depth categories during individual dives, based on the relatively coarse-scale data obtained directly from SRDLs.

Additional depth points were created between transmitted points in order to decrease the differences between individual depth points. Three additional depth points were introduced between each pair of successive recorded points, thereby generating an additional 15 interpolated depth points per dive to complement the 4 transmitted points, plus the two depth points representing the surface at the start and end of each dive (total of 21 depth points) (see Appendix A Fig. A1). These interpolated depth points were based on an assumption of constant swim direction between transmitted points. While it is unrealistic to assume no variance in swim directions between depth points, we expected such variation to be comparatively small given that the transmitted depth points were those of maximum inflection (Fedak et al. 2001). Each depth point was allocated a percentage time passed value (T), further assuming a constant swim speed between transmitted points. Previous investigations have indicated relatively stable ascent and descent rates in dives of southern elephant seals from Macquarie Island (Hindell et al. 1991; 1992), and swim speeds were not expected to vary substantially between transmitted depth points. We identified 14 depth categories for convenient comparison with reported data obtained from time-depth recording devices (see below). Time spent in each depth bin was calculated based on an “if/else” argument in the R statistical/programming environment (R Development Core Team 2008). Accordingly, each depth value (19 depth points per dive, excluding the two surface values) was categorised within one of 14 identified depth categories. The difference between the corresponding T-value for each depth point and the T-value preceding it was then assumed to be the time spent within the specific depth category. For each dive, the sum of T-values was calculated for each depth category, indicating a total amount of time spent within each depth category during the dive. These values were then further summed to provide total amounts of time spent by individuals at various depths during entire migrations. Further details regarding these calculations are reported in Appendix A (Methods).

Time values were categorised into the appropriate depth bins using an “if/else” argument. Depth bins were created in 100 m increments up to a depth of 1 000 m. Increments increased at deeper depths for convenience, because animals generally spent comparatively little time at these depths (see results).

Mark-resighting analyses

Recently weaned elephant seal pups have been marked on Marion Island since 1983 (n = 12371). Each weaned pup on the island has been double-tagged in the interdigital webbing of the hind flippers with uniquely numbered and colour-coded Dal 008 Jumbotag® markers (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom) (see de Bruyn et al. (2008) for specific details). An intensive resighting schedule has been in existence since 1983. All beaches known as elephant seal haulout sites were checked for tagged seals every seven days during the breeding season (mid-Aug to mid-Nov) and every 10 days during the moulting period (mid-Nov to mid-Apr) from 1983 to 1990. From 1990 the resighting effort every 10 days was also extended through the entire non-breeding period (mid-Nov to mid-Aug). For each seal that was resighted, the tag number, tag colour combination, number of tags remaining (one or two), haulout location and date of the sighting were noted.

We calculated the mean percentage time spent hauled out and percentage time spent at sea for each satellite-tagged individual, within the life stage (juvenile, subadult, adult) that the particular animal was satellite tracked. For example, census data was used for the period from reaching sexual maturity (age 3 years) to the present for females that were considered to be sexually mature at the time of SRDL deployment.

Overall environmental use

In order to gain insights into the environments utilised by southern elephant seals over the course of their lifetimes, we extrapolated the data obtained in this investigation for each sex– and age-class to temporal scales that would reflect a life-time perspective more accurately. This exercise required us to assume that animals within our sample exhibited similar depth use patterns for all appropriate migrations, while in the age-class that they were satellite-tagged in (e.g. adult females tracked during post-moult migrations were assumed to make similar use of depth layers in all post-moult migrations they undertook as adult animals). The variation within groups of the same age– and sex-classes, as well as migrations were relatively small in our sample (see results section) and appear to be representative of typical depth use patterns by animals within the identified categories.

Since insufficient data were available for under-yearling (0-1 years) and yearling (1-2 years) animals, we did not incorporate any estimates of habitat use for these age-classes into our analyses. No distinction was made between migrations for subadults inside a year because animals within this age-class often haul out during winter months and do not generally participate in the breeding season haulout (Kirkman et al. 2001).

We calculated the average percentages of time spent in different environments (at sea; on land; diving at sea; at the sea surface; at depth 0-100 m; at depth 100-300 m; at depth 300-700 m, at depth 700-1 500 m; and at depths greater than 1 500 m) by sex, age-class and migration type (i.e. post-moult or post-breeding). These depth categories were chosen to reflect shallow depths (1 category), mid-water depths (2 categories) and deep-water depths (2 categories). Mean percentages of time spent on post-moult and post-breeding migrations per year were calculated for all adult animals. From this data we calculated the mean percentage of time spent per year in each of the environments by animals of the different age-classes and sexes. These annual means were extrapolated up to the estimated mean age beyond which <5% of individuals for any given cohort remain alive (10 years for males and 13 years for females) (de Bruyn 2009).

Data for adult animals were initially divided between migrations. From the mark-resighting data we were able to calculate the relative percentages of time spent by adult animals on post-moult versus post-breeding migrations. Times at depth data were weighted prior to calculations, to reflect the differences in time spent on different migrations. For example, the annual time spent by an adult female (for which 75.75% of the time spent at sea was during post-moult migrations, and 24.25% during post-breeding migrations – see results) at the sea surface (T_{ss}) was calculated as follows:

$$T_{SS} = \frac{[(75.75 \times T_{PM}) + (24.25 \times T_{PB})]}{100}$$

Where T_{PM} = mean percentage of time spent at the sea surface during a post-moult migration

T_{PB} = mean percentage of time spent at the sea surface during a post-breeding migration.

The mean annual percentages of time spent by animals in different age- and sex classes were further extrapolated to provide an indication of time spent in different environments during the course of a seal's lifetime.

Statistical analyses

All filtering, depth binning and statistical analyses were carried out in the R environment (R Development Core Team 2008). Pearson's product moment correlation coefficient statistics were used to test for potential correlations between the various depth use parameters and water depth. Since not all completed dives were successfully transmitted, we calculated daily mean values for each parameter for the correlation analyses. Unless otherwise stated, all results are presented as means ± SD.

Results

Fifty-two tracks returned usable data, after seven devices malfunctioned or were lost at sea soon after deployment. The tracks that returned usable dive data included among others, one under-yearling, one yearling and one adult female without previous haul-out history on the island. Further, one track returned dive data for only 16 days. These tracks were removed from the analysis and are not reported on. The remaining 48 tracks contained three tracks that encompassed both post-moult and post-breeding migrations of the same tagged individuals. We therefore divided these tracks into post-moult and post-breeding migrations, resulting in dive data from a total of 51 migrations of known-aged seals being reported (Table 2.1). Animals were tracked for a median period of 175 days (min = 54; max = 342). Before filtering, these tracks provided 182 751 dive profiles. The filtering process removed 11 360 of these profiles, resulting in a total of 171 391 dive profiles being analysed. Summary results from these dives are reported in Appendix A (Table A1).

Table 2.1: Summary of tracks analysed. Values for days tracked and dives per track are reported as median (range). PM = post-moult migration; PB = post-breeding migration.

Age-class / sex	Migration	n (tracks)	Days tracked	n (dives)	Dives per track
Adult males	PM	5	155 (120-273)	9 458	2 086 (649-3 264)
	PB	4	93.5 (70-99)	7 087	1 835 (1 365-2 052)
Adult females	PM	18	244 (46-332)	88 487	5 386 (699-2 100)
	PB	9	77 (54-130)	15 188	1 750 (616-2 100)
Subadult males		13	205 (77-342)	46 249	3 303 (1 048-8 343)
Subadult females		2	115 (55-175)	4 922	2 461 (885-4 037)

Southern elephant seals from Marion Island spent on average 84.65% (± 5.11) of their time at sea, diving for 91.67% (± 2.08) of this time. Overall, the elephant seals spent 15.35% (± 5.12) of their time hauled out on land, 77.59% (± 4.96) of their time diving and 7.06% (± 1.88) of their time at the sea surface. Adult males spent less time diving, and more time hauled out on land than subadult males and females of either age-class (Fig. 2.1). Subadult males, furthermore, spent more time hauled out when compared to adult females. No differences were observed in time spent hauled out between subadult animals of either sex or between females of both age-classes. Adult animals of both sexes spent more time at the sea surface than subadult animals.

Maximum depths

Adult male elephant seals dived to deeper mean depths than any of the other age- and sex classes, reaching a mean depth of 549.8 m (± 199.2). Subadult males dived to a mean depth of 535.2 m (± 84.1), adult females to 445.3 m (± 65.5) and subadult females to 469.5 m (± 51.4). Despite the substantial differences in maximum dive depths, considerable overlap was evident between age- and sex classes, particularly in areas of deeper water where most animals dived to depths in the region of 500 m (Fig. 2.2). The deepest dives were recorded for an adult male that regularly reached a transmitted depth of 2 149 m. At least 166 dives in excess of 2 000 m were recorded for this individual, before transmissions ceased. Because the resolution of depth values is reduced at greater depths in SRDLs (depth values are rounded to the nearest 32 m at depths greater than 2 000m) (Lovell pers.comm.), the repeated transmitted depths of 2 149 m are an indication of true depths between 2 133 m and 2 165 m.

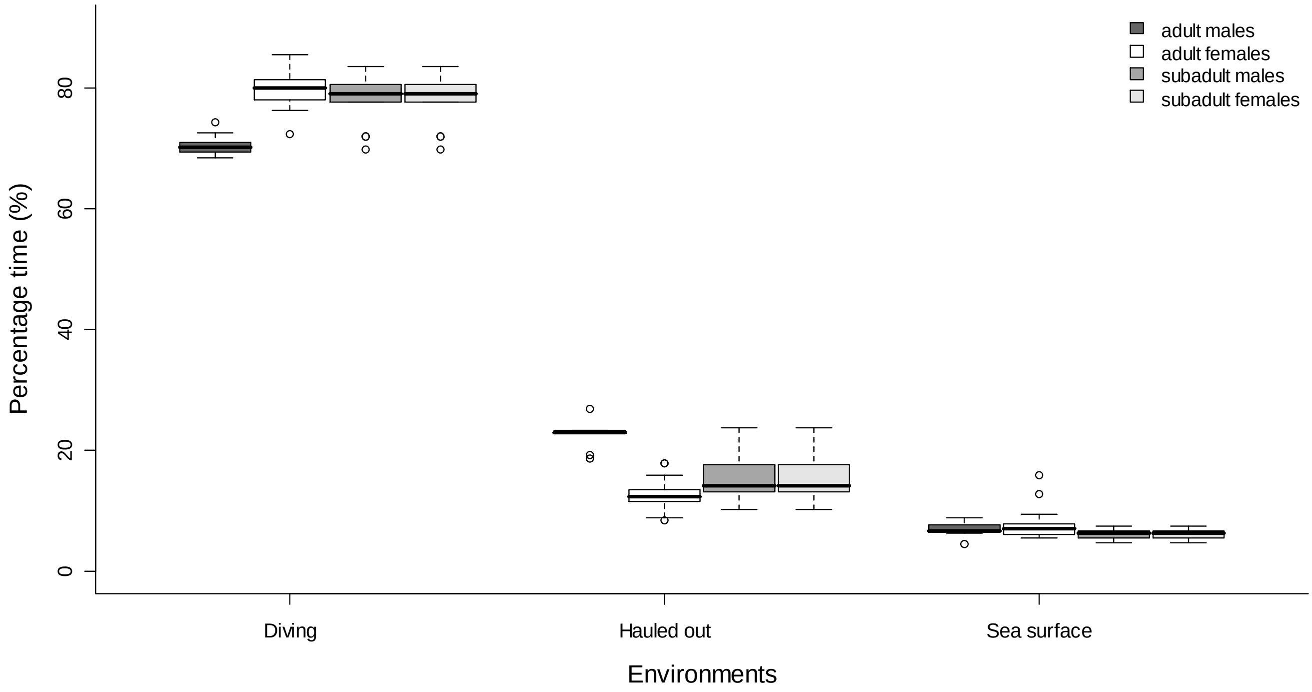

Figure 2.1: Plot indicating total mean percentages of time spent by animals from different age- and sex classes underwater (diving), hauled out on land and at the sea surface.

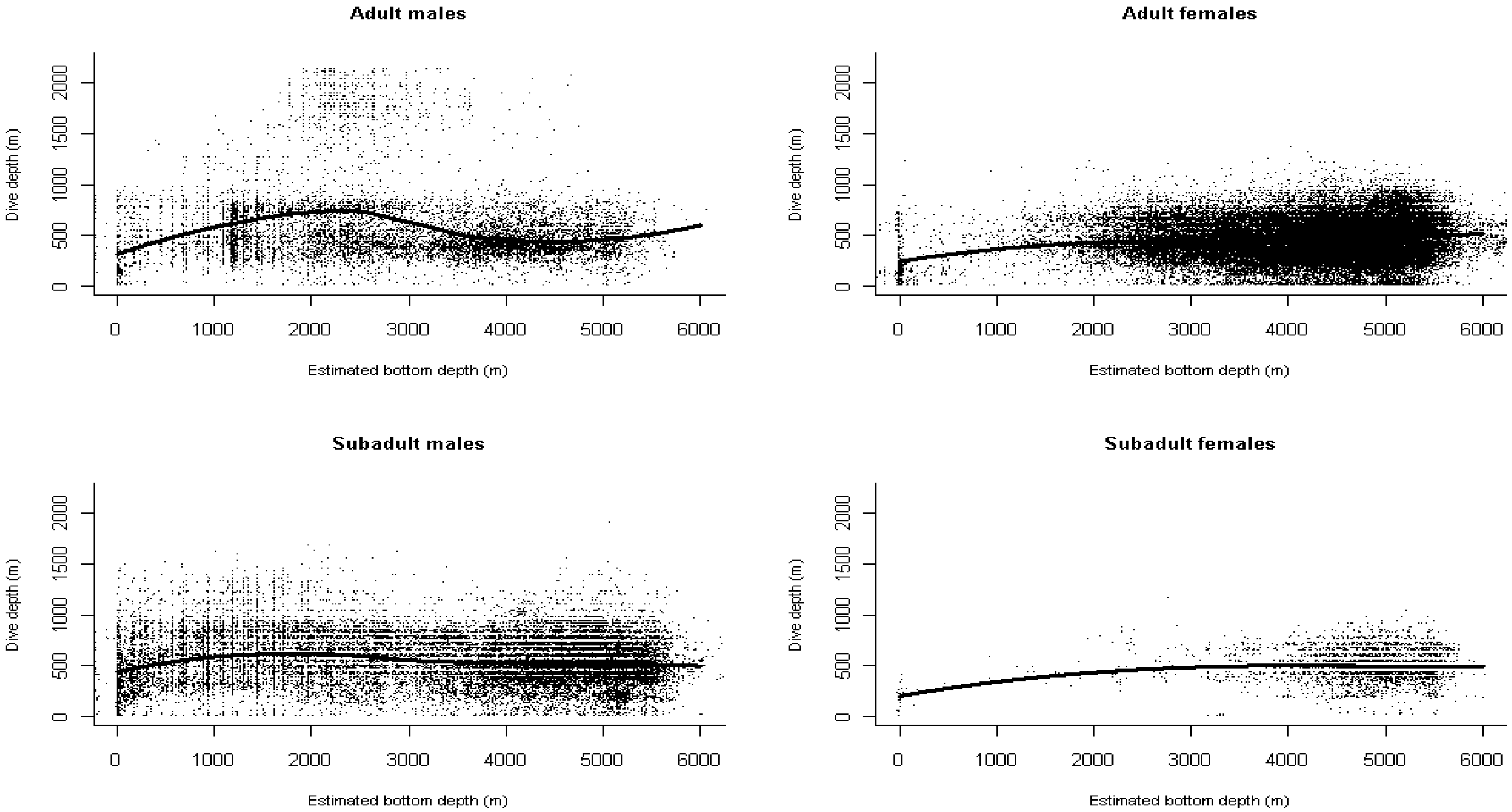

Figure 2.2: Maximum dive depths of southern elephant seals from Marion Island plotted against bottom depth (estimated from the Smith & Sandwell 1997 database). The relatively poor resolution (between 1 and 12 km) of the bathymetry database and location errors associated with the Argos satellite estimates resulted in some error in depth estimates. Therefore some dives appear to be deeper than the bottom depth. Local polynomial regression lines were fitted to each of the groups.

Table 2.2: Summary of mean percentages of time spent in different environments by southern elephant seals of different age- and sex classes from Marion Island.

Environment	Adult males (n = 9) Mean (%)	Adult females (n = 27) Mean (%)	Subadult males (n = 13) Mean (%)	Subadult females (n = 2) Mean (%)
On land	22.6 ± 2.4	12.5 ± 2.5	15.8 ± 4.4	17.8 ± 13.1
At sea	77.4 ± 2.4	87.5 ± 2.5	84.2 ± 4.4	82.2 ± 13.1
While at sea				
Diving	91.1 ± 1.5	91.3 ± 2.5	92.7 ± 1.1	92.7 ± 0.3
At sea surface	8.9 ± 1.5	8.7 ± 2.5	7.3 ± 1.1	7.3 ± 0.3
Overall				
Diving	70.5 ± 1.9	79.8 ± 3	78.1 ± 4.4	76.2 ± 12
At sea surface	6.9 ± 1.3	7.6 ± 2.2	6.1 ± 0.9	6.1 ± 1.2
0-100 m	8.3 ± 1.1	11 ± 3.2	9.3 ± 3.6	10.2 ± 0.8
100-200 m	8.5 ± 2.2	12.4 ± 3	11.1 ± 3.2	12.1 ± 1.3
200-300 m	11.2 ± 2.4	14.3 ± 2.3	11 ± 1.7	14 ± 0.9
300-400 m	17.3 ± 8	14.8 ± 3.2	12 ± 1.9	16.5 ± 1.3
400-500 m	8.9 ± 2.3	12.7 ± 2.6	10.8 ± 2.4	11.6 ± 3.2
500-600 m	5.2 ± 2.2	8.8 ± 3	8.9 ± 2.5	7 ± 5.2
600-700 m	3.7 ± 2.2	4 ± 1.9	5.9 ± 2.3	3.6 ± 4.3
700-800 m	3.7 ± 3.3	1.2 ± 1	4.9 ± 3	0.9 ± 0.8
800-900 m	1.3 ± 1.3	0.5 ± 0.5	2.7 ± 2	0.2 ± 0.1
900-1 000 m	0.5 ± 0.8	0.1 ± 0.1	0.8 ± 0.6	0.1 ± 0
1000-1 250 m	0.6 ± 1.3	0	0.6 ± 0.7	0
1250-1 500 m	0.6 ± 1.5	0	0.1 ± 0.3	0
1500-2 000 m	0.5 ± 1.6	0	0	0
2 000 m +	0.1 ± 0.1	0	0	0

Depth use

Since subadult animals in this study hauled out at varying times during the year (as opposed to specific breeding and moulting haulouts as for adults), we did not distinguish between migrations for subadults and a generalized linear model could therefore not be utilised to compare depth use between age-class, sex and migration. All animals spent comparatively the most time at depths between 300 m and 400 m (adult females = 14.79 ± 3.23%; adult males = 17.28 ± 8.04%; subadult females = 16.47 ± 1.34%; subadult males = 11.96 ± 8.04%) (Table 2.2; Fig. 2.3). Adult females spent more time at mid-water depths (200-500 m) than adult males, while adult males spent more time at deeper depths (700 m and deeper) compared to adult females.

Differences in depth use between migrations by adult animals varied considerably between males and females (Fig. 2.3). Females spent a similar proportion of time in most depth categories irrespective of migration type but post-breeding females spent more time at the sea-surface than post-moult females. Males on post-breeding migrations spent more time at depths between 200 m and 400 m (particularly between 300 m and 400 m), but less time at deeper depths (500-800 m) than males on post-moult migrations.

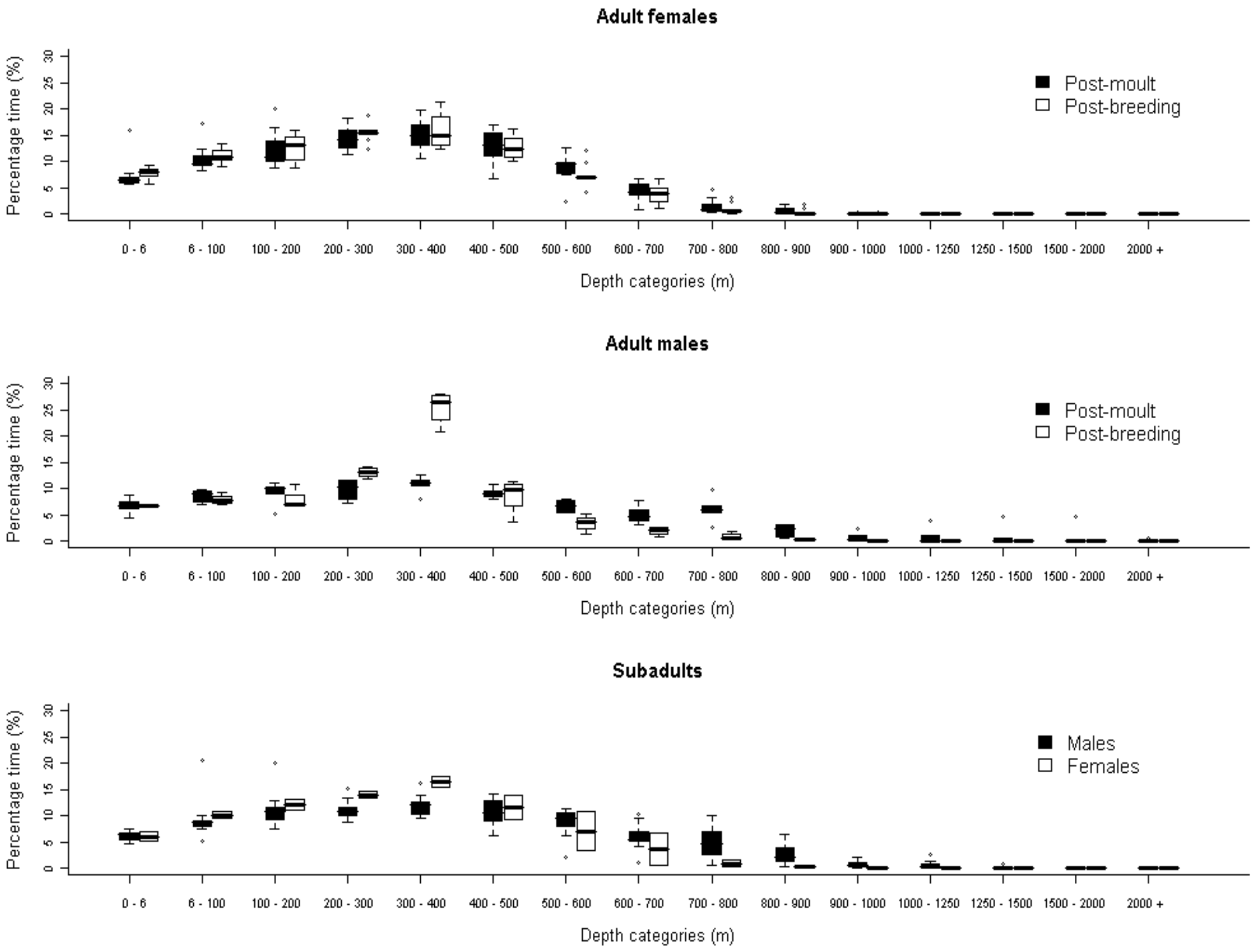

Figure 2.3: Depth use patterns for southern elephant seals of different age- and sex classes hauled out at Marion Island.

Overall environmental use

Differences were observed in relative proportions of time spent between sexes on different migrations. Of the total time spent at sea by adult females, 75.75% was on post-moult migrations, and 24.25% on post-breeding migrations. Adult males also spent relatively more time on post-moult migrations, and less time on post-breeding migrations (71% on post-moult migrations, and 29% on post-breeding migrations), but the ratio of time spent on post-breeding versus post-moult migrations differed to that of adult females. Adult males spent proportionally more time on post-breeding migrations than adult females did, when compared with post-moult migrations.

The mean percentages of time spent by adult and subadult animals of both sexes in various environments are reported in Table 2.2. Adult males spent more time than any other group on land (22.6% of their time); while adult females spent the smallest percentages of time on land (12.53%). Adult females spent the largest proportion of time diving (79.83%), and similar proportions of time were recorded for subadult males (78.09%) and subadult females (76.17%). Adult males spent comparatively the least amount of time diving (70.47%). Animals of all age- and sex classes spent most of their time diving to depths between 300 and 400 m. Males of both age-classes spent more time than females at depths greater than 700 m. Females spent more time than males at depths shallower than 300 m.

The extrapolated mean annual percentages of time spent by animals of either sex during the course of a seal lifetime are reported in Table 2.3. Females spend on average 86.98% of their lives at sea, while males spend less of their lives at sea (80.89%). Females spend an estimated 79.64% of their lives below the sea surface, while males spend 74.38% below the surface. Animals of both sexes spend the majority of their time at sea at depths ranging between 300 m and 700 m – females spending 40.45%, and males 35.78% of their lives at these depths. Males spend more of their lives at increased depths, spending 8.59% of their time at depths between 700 m and 1 500 m.

Depth use in relation to water depth

Dive parameters were rarely correlated with estimates of the water depth at the dive locations. No positive or negative correlation coefficients were more than 0.5 (Fig. A2 – Appendix A), despite various correlations being statistically significant ($p < 0.05$). Mean maximum dive depths of subadult female seals were positively correlated (cor = 0.42; p <

0.001) with water depth. Mean dive durations of subadult females also displayed a similar correlation with water depth (cor = 0.49; p < 0.001).

Table 2.3: Extrapolated estimates of total percentages of time spent within different environments by male and female southern elephant seals from Marion Island over an estimated lifetime (excluding the first two years).

	Females (for total of years 2-13)	**Males (for total of years 2-10)**
	Overall percentage of time	**Overall percentage of time**
At sea	86.98 ± 3.42	80.89 ± 3.39
On land	13.01 ± 3.42	19.11 ± 3.39
Diving	79.64 ± 3.76	74.38 ± 3.11
Sea surface	7.35 ± 1.98	6.51 ± 1.14
0-100 m	10.73 ± 2.48	8.87 ± 2.39
100-300 m	26.63 ± 5.03	20.78 ± 4.44
300-700 m	40.45 ± 10.48	35.78 ± 7.97
700-1500 m	1.84 ± 1.69	8.59 ± 6.49
1500 m +	0.00 ± 0.00	0.39 ± 0.85

Discussion

Marion Island represents one of the northernmost breeding colonies of southern elephant seals, and its distance from the ice edge and remoteness from other land masses require the elephant seals breeding here to adopt a largely pelagic lifestyle. We quantify the extreme lifestyle that southern elephant seals lead by illustrating what proportions of their lifetimes are spent in various environments that pose vastly different physiological challenges. A male seal would cumulatively have spent a total of approximately 2 362 days at sea; 2 172 days below the sea surface; 259 days at shallow depths (0-100 m); 607 days at depths between 100 m and 300 m; 1 045 days between 300 m and 700 m; and 262 days at depths below 700 m, between the ages of 2 and 10 years (~ 2 920 days). Clearly, spending your time in one extreme environment for the duration of your life requires completely different physiological adaptations to spending different proportions thereof in numerous environments. For example, while a bottom dwelling fish would spend 100% of its lifetime in a certain depth environment, in contrast consider the challenges that an average male elephant seal faces by spending perhaps three years (1 045 / 2 920 days = 36%) of its' 10-year long life at about 500 m below the sea surface, but then also one-and-a-half years (558 / 2 920 days = 19%) of its life on land.

Comparatively, a 10 year old female would have spent (from age two) 2 535 days at sea; 2 321 days below the sea surface; 313 days at shallow depths (0-100 m); 777 days at depths between 100 m and 300 m; 1 179 days between 300 m and 700 m; and 55 days at depths below 700 m. These values imply superb adaptation to a varied three-dimensional marine environment in addition to their ubiquitous (and often strenuous) existence on land.

Southern elephant seals from Marion Island spend more than 65% of their lifetimes at water depths deeper than 100 m, a result that is not surprising given food consumption estimates for this species (Carlini et al. 2005) and their obvious requirements to maximise food intake. Females spend comparatively more time at mid-water depths than males, and males spend more time at increased depths in excess of 700 m. This is in contrast to previous findings where mean maximum dive depth recorded for elephant seals from Macquarie Island indicated that males tend to perform shallower dives than females (Hindell et al. 1992), a probable result of benthic feeding over the Antarctic continental shelf by males there (Hindell et al. 1991).

Maximum depths

The variation in maximum dive depths attained by male elephant seals from Marion Island suggests predominantly pelagic feeding habits with occasional benthic dives, sometimes in excess of 2 000 m. One adult male seal (14 years old) repeatedly attained dive depths in excess of 2 000 m, which are to our knowledge, the deepest recorded air-breathing vertebrate dives to date. Repeated depth measurements of 2 149 m, interspersed by shallower depths, indicated that a number of dives were at least deeper than 2 133 m. Female elephant seals from Marion Island displayed exclusive pelagic diving behaviour – a result that appeared to conform with results obtained for females from other southern elephant seal populations, although this may be dependent on the depth of the benthos around the haulout locations (Hindell et al. 1991; Campagna et al. 1995). The deep waters surrounding Marion Island therefore allows elephant seals of both sexes to dive more often to depths in the region of 500 m, particularly over very deep water (in excess of 3 000 m) than any other depth (Fig. 2). Plots of maximum dive depths over time of day (UTC) revealed some diurnal variation in dive depths for all age- and sex classes, with the deepest dives apparently occurring during daylight hours (Jonker & Bester 1994; unpublished data), although no attempts were made to control for potential effects of geographic position and seasonality.

Environmental use

The combined time at depth data for individual animals, and mark-resighting data of these animals from birth enabled the description of environmental use by southern elephant seals over an unprecedented temporal scale. Over their subadult and adult lifetimes, southern elephant seals spend more time between 300 m and 400 m water depth than any other environment. Male elephant seals from Marion Island spend smaller proportions of their time at sea (approximately 81%) than females (approximately 87%), though males spend substantially more time at depths deeper than 700 m (approximately 9% vs. 2%). The physiological implications of the long-term (but not permanent) exposures of elephant seals to such great depths are difficult to surmise (Kooyman 2006). While some species spend their entire lives at these depths, elephant seals are necessitated to spend considerable periods of time completely hauled out of the water. This diversity of habitat use obviously requires special adaptations. Such adaptations for long and deep diving in marine mammals are varied (Ramirez et al. 2007) and include high concentrations of haemoglobin in blood (Ridgway & Johnston 1966) and myoglobin in skeletal and heart muscle (Polasek & Davis 2001) to increase oxygen storage capacity; lung collapse and stiffened, yet compressible tracheas (Falke et al. 1985; Bostrom et al. 2008); metabolic rate reductions (Kooyman & Ponganis 1998); changes in cardiac output during dives (Fahlman et al. 2006) and even increased resistance to hypoxia in neuronal tissues (Folkow et al. 2008; Mitz et al. 2009). Furthermore, Meir et al. (2009) recently showed that northern elephant seals (*Mirounga angustirostris*) virtually exhaust blood oxygen levels during routine dives and that elephant seals tolerate extreme hypoxemia during diving.

The potential long-term effects of the extreme diving patterns presented here are unknown. Southern elephant seals have relatively short lifespans for animals of such large size, with breeding males from Marion Island generally not ageing beyond ~ 12 years (oldest male recorded: 14 yrs old), and relatively few females attaining ages greater than 15 years (oldest female recorded breeding at age 20) (de Bruyn 2009). While their extreme reproductive behaviour is likely to significantly reduce their life spans, previous studies have suggested possible long-term negative effects of continuous deep diving in animals previously thought immune to the effects of deep diving, notably sperm whales (*Physeter macrocephalus*) (Moore & Early 2004; Rothschild 2005). Similar evidence for decompression related pathology have also been reported for plesiosaurs, thought to have been deep-diving vertebrates (Rothschild & Storrs 2003). While no such evidence exists for southern elephant seals, the generally short life spans (Le Boeuf & Laws 1994b) may be further influenced by negative effects associated with continuous, deep diving. Notably, proportionally fewer Marion Island elephant seals appear to attain breeding ages in excess of 13 (males) and 16 years (females) (de Bruyn 2009), respectively, than has been recorded at other larger populations such as Macquarie Island (Hindell 1991). Elephant seals, particularly adult males, from Macquarie Island generally perform shallower dives than animals from Marion Island – adult males hauled out Macquarie Island were reported to dive to mean dive depths of 398 m (± 164) (Hindell et al. 1991), compared to 550 m (± 199) (this study). Adult females from Macquarie Island reportedly dived to more similar depths as females from Marion Island (Macquarie: 423 m ± 200; Marion: 445 m ± 66). Again, dives of adult males from Macquarie Island were shorter than dives recorded for Marion Island males (Macquarie: 24 min ± 9.2; Marion: 32.4 min ± 11.5), while dive durations of adult females were similar (Macquarie: 27.1 min ± 12.1; Marion: 26.3 min ± 11.1). We therefore propose a "deeper diving – shorter life" hypothesis that a greater frequency of dives to relatively greater depths will have a negative survival consequence as a result of repeatedly increased physiological stress associated with such deep diving. This hypothesis requires further investigation to elucidate the effects of increased physiological stress (as a consequence of more time spent at depth) on the differences in population dynamics (McMahon et al. 2003; de Bruyn 2009) between the Marion Island and other elephant seal populations.

Water depth and sea ice influences

Relationships between dive behaviour and water depth have been reported for southern elephant seals from other populations, notably Peninsula Valdés where seals often target areas of both shallow and deeper water depths (e.g. the Patagonian shelf and Argentine basin) (Campagna et al. 2007). We found little correlation between the various depth parameters calculated and the water depth available to the study animals. This is likely due to most of the migrations targeting areas with bottom depths that exceed the diving capacity of the study animals. Similarly, the dive behaviour of elephant seals from other populations seems to be influenced by the presence of sea ice (Bornemann et al. 2000; Bailleul et al. 2007a). Subadult animals from King George Island appear to avoid high concentrations of sea ice, while adult females from Kerguelen Island apparently shifted northwards of the expanding sea ice during the austral winter. Animals from Marion Island have, however, only rarely been recorded to travel as far as the Antarctic continental shelf (Jonker & Bester 1998; Tosh unpublished data) and therefore do not often exploit resources associated with sea ice. The differences in geographic locations of migrations between southern elephant seal populations are likely to result in differences in depth use pattern between specific age- and sex classes of such populations. For instance, adult male seals from populations where males are reported to target continental shelves or other areas of shallow depth (e.g. Kerguelen Islands, Peninsula Valdés, South Georgia, Macquarie Island, and King George Island) are likely to spend smaller proportions of their lives at depths greater than 1 000 m when compared to animals from Marion Island. Conversely, adult females from Marion Island appear to display dive behaviour that is more conservative and consistent with reported migrations from some other populations (Hindell et al. 1991; Campagna et al. 1995), resulting in reduced differences in depth use of adult females amongst populations.

Sex and migration effects

Male southern elephant seals can be up to ten times larger than female southern elephant seals (Le Boeuf & Laws 1994b). This increased body size, and resulting muscle mass, may explain the lack of variation in diving behaviour amongst females and the observed variation and extremes encountered by male southern elephant seals in this study. Male elephant seals dive deeper than females and spend substantially more time in deeper water (Fig. 2.3). The difference in time spent at depth observed in this study may point towards differences in prey species targeted by the two sexes of elephant seal from Marion Island. Stable isotope ratios obtained from animals hauled out at Peninsula Valdés indicated that prey choice and trophic levels of prey targeted by females was different to those targeted by males (Lewis et al. 2006). Males from this population evidently showed a very broad range of prey choice in varying trophic positions, while females seemed to target a more restricted range of prey. Previous studies suggested a peak in biomass per volume at depths between 1 500 m and 2 300 m in areas associated with mid-ocean ridges (Sutton et al. 2008), such as the South West Indian

Ridge along which Marion Island is situated. Male elephant seals may thus be physiologically more capable of exploiting higher densities of prey at greater depths. Increased energetic demands due to large body size and life history requirements may also drive varied foraging strategies.

Adult male southern elephant seals from Marion Island haul out earlier than females during the breeding season to establish territories and thus spend comparatively less time diving at sea and more time hauled out on land. The results obtained in this study are limited to breeding adult male southern elephant seals and the converse may be true for non-breeding adult males that presumably have less stressful lives and longer life expectancies (Le Boeuf & Laws 1994b). The differences observed in depth use during the post-moult (austral winter: February to October) and post-breeding (austral summer: November to January) migrations may arise from the different durations and locations of the migrations. Location data indicated that three males on post-breeding migrations tended to move along the South West Indian Ridge, while males on post-moult migrations displayed more variation in migration locations (Tosh unpublished data). Notably, the adult males tracked during their post-breeding migrations spent considerably more time between 300 m and 400 m depth (Fig. 2.3). Since all of these animals concentrated their movement along the South West Indian Ridge, and were there during the same time period, it is likely that they were exploiting a food resource present in this depth layer at the time.

Adult females spent less time during the post-moult migration at the sea surface and in shallow depths (0-100 m), than during their post-breeding migrations. Diel variation in dive depths was more pronounced during post-moult migrations for adult females and adult males, when compared to post-breeding migrations (unpublished data). This likely influenced the overall times spent by animals in various depth categories and may further explain some of the variation in depth use between migrations. Subadult elephant seals spent less time at the sea surface than adults, presumably minimising predation risk. Killer whales are known to predate on southern elephant seals in the vicinity of Marion Island (Pistorius et al. 2002; Tosh et al. 2008). As killer whales are not known to dive deeper than approximately 300 m (Baird et al. 2005), minimising the amount of time spent at the sea surface would probably confer some advantage to younger (and presumably more at risk) elephant seals. This mode of predator avoidance has been reported for northern elephant seals (Le Boeuf et al. 2000).

Conclusion

By combining data from a long-term mark-resighting experiment with concurrent deployments of satellite-linked data loggers, we report the closest possible approximation of habitat use in southern elephant seals across their lifespans. A lifetime divided between the physiological stresses of several markedly different environments may incur fundamental fitness costs in terms of reproduction and longevity to southern elephant seals. We illustrate for the first time the full extent of use of these vastly different habitats to allow for more informed future discussion of the physiological adaptations relevant to individual survival, and the consequences thereof on population demographic parameters. Vertical habitat use of southern elephant seals from Marion Island reflects the habitat of animals that are mostly dependent on pelagic prey. The diving behaviour of Marion Island southern elephant seals also illustrates the impact of sexual dimorphism in this species, irrespective of locality. However, we propose the “deeper diving – shorter life” hypothesis (for future investigation) relating the survival probabilities of Marion Island’s male elephant seals (in particular) with their deeper mean depth-use, compared with elephant seals from populations that utilise shallower, benthic foraging locations. Furthermore, lifetime monitoring of the foraging movements of the satellite-tagged animals in this study will clarify potential long-term influences of individual dive behaviour on growth, survival and reproductive performance.

CHAPTER THREE: WATER COLUMN USE AND FORAGE STRATEGIES OF FEMALE SOUTHERN ELEPHANT SEALS FROM MARION ISLAND*

Abstract

The at-sea behaviour of marine top predators provides valuable insights into the distribution of prey species and strategies used by predators to exploit patchily distributed resources. We describe the water column usage and dive strategies of female southern elephant seals from Marion Island tracked between 2004 and 2008. Dives representing increases in forage effort were identified using a method that combines dive type analyses and the calculation of relative amounts of time that animals spend in the bottom phases of dives. Results from this analysis indicate that female elephant seals from Marion Island tend to display lower levels of forage effort closer to the island and display intensive opportunistic forage bouts that occur at a minimum distance of approximately 215 km from the island. Females from Marion Island dived deeper and for longer periods of time, compared to females from other populations. Most animals displayed positive diel vertical migration, evidently foraging pelagically on vertically migrating prey. A few animals displayed periods of reverse (negative) diel vertical migration however, diving to deeper depths at night, compared to daytime. This behaviour is difficult to explain and prey species targeted during such periods unknown. Our results illustrate plasticity in foraging behaviour of southern elephant seals, as well as inter-population differences in forage strategies.

*Published as: McIntyre, T., Bornemann, H., Plötz, J., Tosh, C.A. & Bester, M.N. (in press) Water column use and forage strategies of female southern elephant seals from Marion Island. *Marine Biology* doi: 10.1007/s00227-011-1719-2

Introduction

The ability of top predators in the marine environment to locate and exploit often patchily distributed food resources is key to their reproductive success and survival. This is particularly true in the Southern Ocean which, despite being one of the most productive oceans (Smetacek & Nicol 2005), is characterised by broad- and fine-scale spatio-temporal fluctuations in various physical properties (Rintoul et al. 1997) that influence the distributions and abundance of biological communities (Rodhouse & White 1995). Recent studies have often focussed on the identification of productive foraging areas for marine predators, where prey availability is presumably elevated (Gende & Sigler 2006; Bestley et al. 2010; Scott et al. 2010). Such investigations further aim to explain the bio-physical properties of such areas, their importance to the marine ecosystem and top predators in particular, as well as their management and conservation implications (Sydeman et al. 2006).

Southern elephant seals (*Mirounga leonina*) are considered useful indicator predator species for the Southern Ocean, largely due to their circumpolar distribution (Le Boeuf & Laws 1994b), deep diving and wide-ranging habits (Hindell & McMahon 2000), as well as their roles as major consumers of second-order producers (Bradshaw et al. 2003; Carlini et al. 2005). Population numbers of southern elephant seals have been unstable, with various sub-populations experiencing decreases in numbers since the 1950s (Le Boeuf & Laws 1994b; McMahon et al. 2005). The southern elephant seal population of Marion Island underwent one of the most dramatic declines, but has now apparently stabilised, and even increased in recent years (Pistorius et al. 1999; McMahon et al. 2005; de Bruyn 2009). Reasons for this decline are not completely understood, but one of the hypotheses is that changes in adult female survival appear to have played a significant role (Pistorius et al. 2004; Pistorius et al. 2008a; 2008b). Food limitation has been inferred as one of the most important factors influencing the Marion Island population and adult female survival in particular (Pistorius et al. 1999; 2001; 2004; Tosh 2010).

Marion Island is one of the northernmost breeding colonies of southern elephant seals (Le Boeuf & Laws 1994b). The distance from the ice edge, continental shelves and other shallow bathymetric features result in the exposure of animals from Marion Island to very deep pelagic environments. Adult southern elephant seals normally haul out on land twice a year - once for the breeding season when animals give birth, wean their young, and mate (austral spring), and once for the obligatory moult (austral summer) (Le Boeuf & Laws 1994b). Early investigations into the ranging and diving behaviour of female southern elephant seals from Marion Island indicated much variation in individual strategy of animals, both in the oceanographic areas targeted and individual dive behaviour (Bester & Pansegrouw 1992; Jonker & Bester 1994; 1998). More recent investigations into the migration patterns of elephant seals from Marion Island, however, showed more predictable travel directions (predominantly south-west of the island), although individual variation in migration strategies was also evident (Tosh 2010).

Methods to identify areas of increased foraging effort in animal tracks are varied and include different levels of sophistication (Robinson et al. 2007). Track-based methods include the comparatively simple identification of areas of restricted search based on track variables such as turning rate, residency and transit rate (Le Boeuf et al. 2000; McConnell et al. 2002), as well as changes in distance from origin (Tosh et al. 2009). Computationally more intensive procedures include the use of first passage time (Fauchald & Tveraa 2003), fractal dimensions (Tremblay et al. 2007) and kernel density calculations (Worton 1989). Recently, more complicated modelling approaches were employed, including state-space models (Patterson et al. 2008; 2009). Bailleul et al. (2008) incorporated the vertical behaviour of diving animals into first passage time analyses to refine estimates of area restricted search in elephant seals from the Kerguelen archipelago. This method used a regression analysis of dive depths, durations and the amount of time spent at the bottoms of dives to identify dives with greater- or lesser-than-expected bottom times (based on the regression residuals). Dives with positive bottom time residuals are assumed to be dives with greater-than-average forage effort. The bottom time residual method does not take into account variations in dive types displayed by elephant seals however (Hindell et al. 1991; Jonker & Bester 1994). This is important when using coarse-resolution data that depicts dives through a limited number of time-depth points (usually 4 per dive), such as that obtained from satellite-relay data loggers (SRDLs) (Sea Mammal Research Unit, University of St. Andrews, Scotland). Calculations of bottom time for dives that display irregular time-depth relationships (i.e. with multiple ascent and descent phases) are then prone to error, since the number of time-depth points is insufficient to capture the entire complicated time-depth profile. These calculations become more reliable, however, if the individual dive profiles are comparatively uncomplicated and display single descent-, bottom- and ascent phases.

Here we describe the vertical water column usage of female southern elephant seals from Marion Island during different seasons. For this purpose we classified dives according to time-depth profiles into predefined dive shapes with expected functions. We then describe areas of increased forage effort as identified by the bottom time residual method, restricted to specific dive types with relatively uncomplicated time-depth profiles.

Methods

A total of 32 satellite-relay data loggers (SRDLs) (Sea Mammal Research Unit, University of St. Andrews, Scotland) were deployed on female southern elephant seals hauled out at Marion Island between April 2004 and November 2008. Deployments were on females of known age and birth-site, born and double flipper-tagged on the island as part of a long-term mark-recapture experiment (Bester 1988b; de Bruyn et al. 2008). Two SRDL models were used in this assessment, namely Series 9000 SRDLs (measuring temperature in addition to dive profiles) and CTD-SRDLs (additionally obtaining conductivity profiles). SRDLs transmitted abstracted dive profiles (Fedak et al. 2001) and temperature profiles with an accuracy of approximately 0.005°C via Service Argos (Argos 1996). Sampling frequency and data abstraction procedures onboard the devices to obtain dive and temperature profiles are detailed in Boehme et al. (2009). Position estimates obtained via Service Argos were used to obtain interpolated positions for each dive profile based on times of data collection by the manufacturers (Boehme et al. 2009). Devices were glued to the cranial pelage of immobilised (Bester 1988a) elephant seals, using quick-setting epoxy glue (chapter 2). All dive data and related meta-information are available in via the PANGAEA information system (http://www.pangaea.de).

Tracks

We employed a simple filtering algorithm to remove estimated locations that required swim speeds in excess of 3.5 m/s and/or creating spikes in the track with angles smaller than

15° and 25° with extensions greater than 2 500 m and 5 000 m respectively (McConnell et al. 1992; Freitas et al. 2008). Filtered tracks were plotted using ArcGIS 9.2 (ESRI, Inc.). Minimum convex polygons (MCPs) of combined tracks for specific time periods were calculated using the Hawth’s Analysis Tools (Version 3.27 © 2002-2006) extension.

Dives

Dives were defined as excursions below the sea surface deeper than 6 m. Local time values, and local times of sunset and sunrise were calculated for each transmitted dive using the ‘maptools’ package (Lewin-Koh & Bivand 2008) in the R environment (R Development Core Team 2008), taking the estimated geographical position of each dive into account. Each dive was accordingly labelled as having occurred either during the day, at night, during sunrise (within 30 min of the local sunrise time) or sunset (within 30 min of the local sunset time). Since differences in dive parameters between day- and night-time were of interest in this investigation, dives recorded during sunrises and sunsets were excluded from further analyses.

SRDLs provide abstracted profiles of individual dives consisting of the deepest depth recorded per dive and three other depth points representing the points of greatest inflection (Fedak et al. 2001), as well as values of dive duration. We calculated the estimated amount of time spent at the bottom of each dive (bottom time), defined as the time spent at depths within 20% of the maximum depth point for each dive (Schreer et al. 2001; Burns et al. 2008). Since elephant seals are known to display diel variation in dive depths and dive durations (Jonker & Bester 1994; Bennet et al. 2001), we separated dives undertaken during daytimes from those recorded at night, before doing the regression analyses. Various dive types have been identified in elephant seals, based on their time-depth relationships and results obtained from deployed accelerometers (Hindell et al. 1991; Jonker & Bester 1994; Biuw et al. 2007; Photopoulos 2007; Mitani et al. 2009). In our study abstracted profiles of dives were classified into six types, namely square (SQ), root (R), drift (DR), U-shaped (U), V-shaped (V), and wiggle (W) dives (Fig. 3.1). The choice of dive types followed Hindell et al. (1991). This was done using a method that employs Breiman’s random forest algorithm (Breiman 2001) for classification purposes (Biuw unpublished). We used the random forest (RF) tree-building method implemented in the “randomForest” package in R (Liaw & Wiener 2002). A manually classified training dataset was first set up and used to classify the remaining dives in R, using the randomForest function. The RF classification generates independent trees, using a bootstrapped sample of the data. A random set of four variables is selected for each node and 1 000 trees grown per split (Photopoulos 2007). A total of 18 variables were selected for the RF classification (Table 3.1).

While both U- and W-shaped dives were assumed to mostly include dives with a foraging purpose (given that more than 95% of all dives were classified as one of these two types – see Results), the relatively low resolution dive profiles did not allow for accurate calculations of bottom time in W-shaped dives. We therefore restricted analyses to "U-shaped" dives, since these were the most numerous dive types identified and their uncomplicated time-depth profiles allowed for reliable calculations of bottom time. A linear regression analysis on the U-shaped dives for each track (calculated separately for day- and night-times) quantified the relationship between bottom time, dive duration and maximum depth of each dive. Using the residual values obtained from the regressions, we were then able to identify each dive as either having a shorter-than-average or greater-than-average bottom time, providing an indication of "forage effort" (Bailleul et al. 2008).

Estimates of bottom depth were extracted from the GEBCO Digital Atlas, GDA, (IOC et al. 2003) for each daily averaged location estimate of each track. Data were exported to ArcMap 9.2 (ESRI, Inc.), converted to raster format and interpolated individual depth estimates extracted using the 'Spatial Analyst Tool'.

Table 3.1: Dive parameters selected for the random forest dive classification.

Dive Parameter	Definition
Dive duration	Duration of a dive (sec)
Maximum dive depth	Depth at inflection point with deepest dive
Bottom depth	Bathymetry depth estimate
Pr1.4; pr1.3; pr2.4	Proportion of dive time spent between inflection points 1 and 4; 1 and 3; 2 and 4
signs	Directions of swimming between inflection points (up, down and stable)
des	Descent rate
asc	Ascent rate
Slope1; Slope2; Slope3	The rate of descent or ascent between point 1 and 2; 2 and 3; 3 and 4
Mean1.4; Mean1.3; Mean2.4	Mean rate of vertical change between inflection point 1 and 4; 1 and 3; 2 and 4
SD.1.4; SD.1.3.;SD.2.4	Standard deviations of the three above

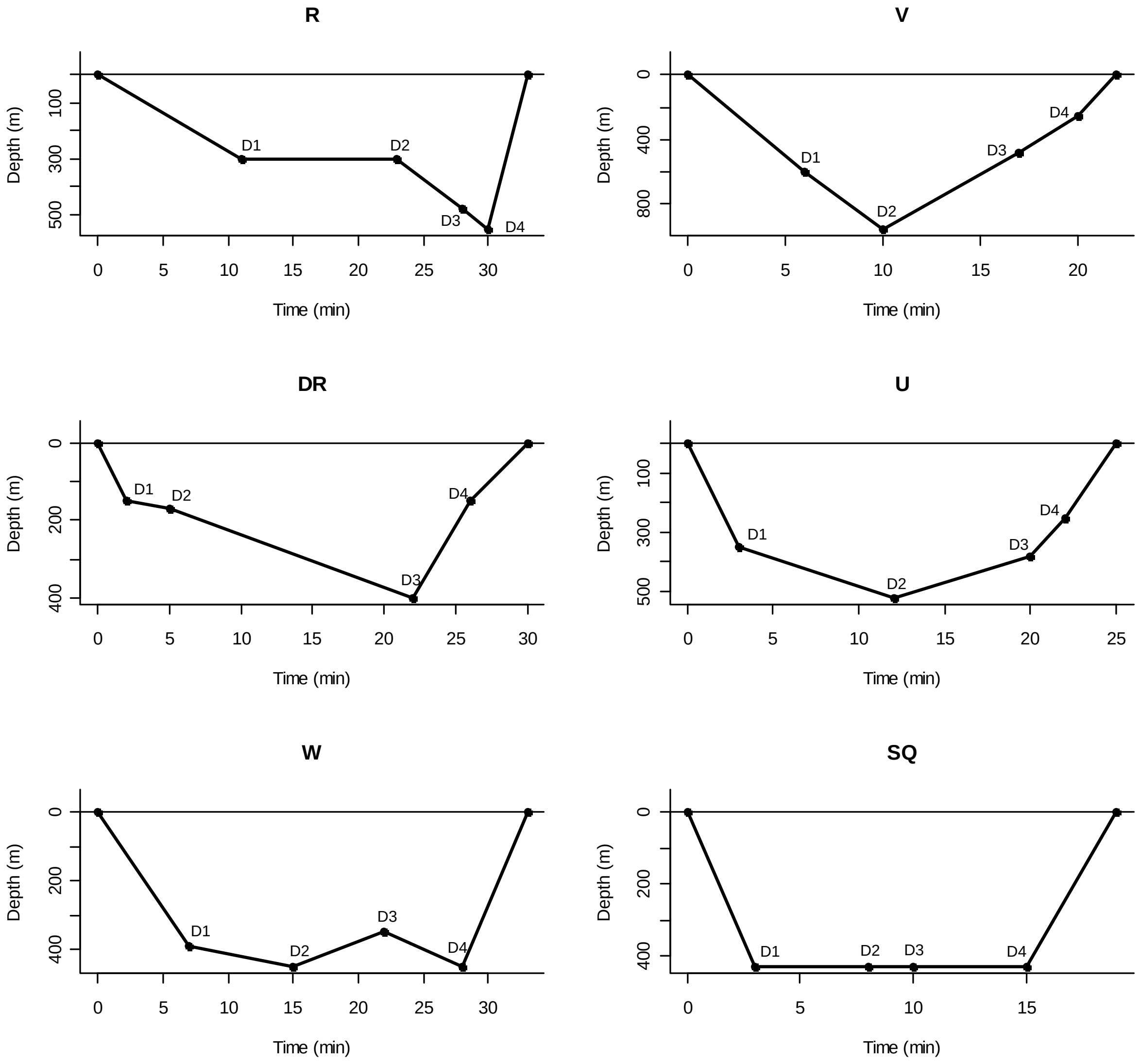

Figure 3.1: Examples of the six dive types distinguished in this study. D1-D4 indicates the four resulting inflection points transmitted by the SRDL after compression of individual dives.

Daily averaged values of dive parameters, distinguishing between daytime and night-time dives, were calculated for each track. These included the mean amounts of time spent at the surface between dives (Surf.Dur$_{DAY}$ and Surf.Dur$_{NIGHT}$), dive durations (Dive.Dur$_{DAY}$ and Dive.Dur$_{NIGHT}$) and dive depths (Dive.Dep$_{DAY}$ and Dive.Dep$_{NIGHT}$). We further calculated the ratio of U-shaped dives with positive bottom time residuals vs. U-shaped dives with negative bottom time residuals (rUBT$_{DAY}$ and rUBT$_{NIGHT}$) per day. This was done to provide an overall indication of forage effort per day and day-stage. rUBT$_{DAY}$ and rUBT$_{NIGHT}$ were mapped for different migration stages (post-moult and post-breeding). Nearest neighbour interpolation was used in ArcMap 9.2 (ESRI, Inc.) to generate raster outputs highlighting areas with different mean rUBT_{DAY} and $\text{rUBT}_{\text{NIGHT}}$ within each MCP at a 0.25° grid scale. We visualised patterns of diel variation in dive depths by calculating the mean daily- and weekly differences in dive depths between day- and night-times, and generating time series plots for each track.

Dive analyses were undertaken in the R environment (R Development Core Team 2008), as well as Microsoft Office Excel ® 2007. Unless otherwise indicated, mean values ± standard deviations are reported. Statistical significance was set at $p \leq 0.05$.

Results

Four devices did not return useful data due to device failure early during migrations. Data from two other devices were removed from the analyses – one provided dive data but failed to provide location data, while the other time-series was considered too short (16 days) to be representative of a migration. Data were therefore retained from 26 devices. Some devices continued to function through two migrations (post-moult and post-breeding), and a few individual seals were instrumented multiple times, resulting in data obtained for 30 migrations undertaken by 18 individuals. Few tracks were available for 2004-2006 and we therefore pooled data to compare the overall dive behaviours between post-moult (PM) migrations and post-breeding (PB) migrations. Animals ranged in age between 2.6 and 10.6 yrs of age at the time of deployment. Standard lengths were not recorded at every deployment, but ranged between 210 and 254 cm (n = 19) when measured.

Tracks

Most animals travelled in a westerly direction away from Marion Island during both PM and PB migrations, while a few animals travelled in south-westerly directions (Figs. 3.2 and 3.3). Females evidently crossed fronts, such as the Sub-Antarctic Front (SAF) to the north and the Antarctic Polar Front (APF) to the south regularly during their migrations. The majority of tracks were confined to areas south of the SAF however. PM migrations tended to extend further away from the island than PB migrations (mean maximum distance from Marion

Island: PM = 2 408 ± 852 km; PB = 1 394 ± 421 km). MCP maps indicated that females tended not to travel further west than 0°E and that migrations sometimes (though not normally) extended as far as the Antarctic Continental Shelf (approximately 68°S). PB migrations did not extend further west than 13°E, and also not further south than approximately 57°S.

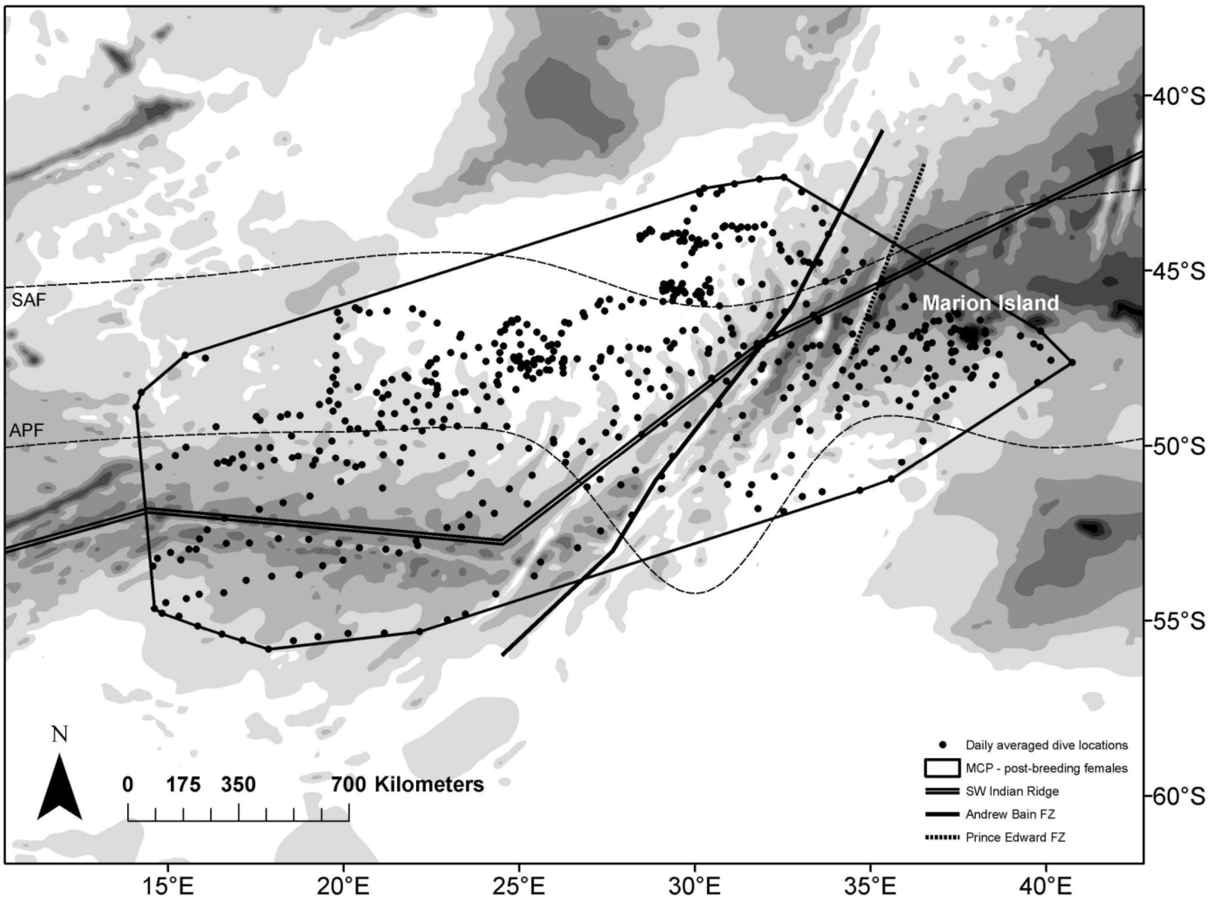

Figure 3.2: Map indicating plots of daily averaged position estimates obtained from female southern elephant seals tracked during post-breeding migrations. A minimum convex polygon (MCP) indicates the area of utilisation. Approximate positions of the Antarctic Polar Front (APF) and Subantarctic Front (SAF) are indicated (from Belkin & Gordon 1996).

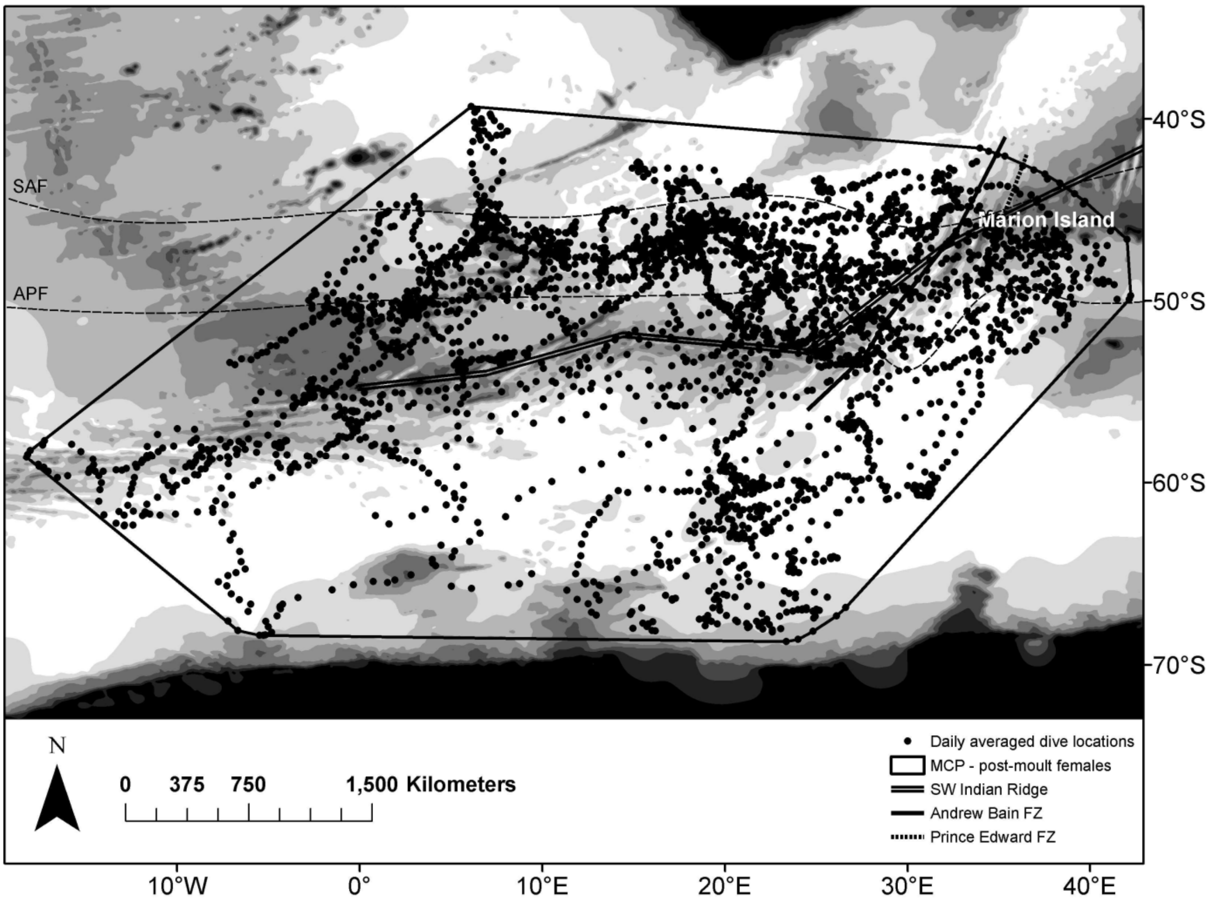

Figure 3.3: Map indicating plots of daily averaged position estimates obtained from female southern elephant seals tracked during post-moult migrations. A minimum convex polygon (MCP) indicates the area of utilisation. Frontal positions are the same as for Fig. 3.2.

Dive behaviour

A total of 108 557 dives in 4 150 track days were recorded (summary data reported in Table 3.2). Mean track lengths were 143 ± 84 days, and consisted of 3 743 ± 2 405 dives. Devices successfully transmitted a mean number of 10.4 ± 6.6 dives during daytime and 14.6 ± 6.7 at night. Females dived to mean depths of 552.2 ± 170.2 m during daytime, and mean depths of 391.2 ± 152.8 m at night. Such dives lasted for 29.4 ± 11.5 min during the day and 24 ± 10 min at night. Overall, post-moult dives were longer (PM = 27.36 ± 11.14 min; PB = 20.15 ± 7.1 min; $t = -106.8$, $df = 30286$, $p < 0.001$) and deeper (PM = 460 ± 177.9 m; PB = 450.2 ± 170.5 m; $t = -6.6$, $df = 21707.4$, $p < 0.001$) than post-breeding dives.

Table 3.2: Summary of dive statistics of female southern elephant seals. Values are reported as mean ± SD. Surf.Dur = surface duration; Dive.Dur = dive duration; Dive.Dep = dive depth.

	OVERALL		PM		PB	
	DAY	NIGHT	DAY	NIGHT	DAY	NIGHT
n	40 813	59 466	32 635	53 423	8 178	6 043
Surf.Dur (min)	2.24 ± 0.77	2.2 ± 0.9	2.25 ± 0.8	2.2 ± 0.9	2.23 ± 0.67	2.08 ± 0.87
Dive.Dur (min)	29.38 ± 11.49	24.02 ± 10	30.9 ± 11.88	24.92 ± 10.01	23.32 ± 7.03	16.11 ± 5.31
Dive.Dep (m)	552.2 ± 170.1	391.2 ± 152.8	560.8 ± 170.8	394.8 ± 153.5	517.8 ± 162.9	359 ± 142.5

Summaries of dive data obtained from individual tracks are reported in Table 3.3. Most animals displayed a positive diel pattern in dive depths and durations, with daytime dives being deeper and longer than night-time dives (for example – see Fig. 3.4). Two animals displayed periods of reverse (negative) diel variation during three migrations undertaken in 2007 (PO043_1 and GG335_1a + 1b), with night-time dives being deeper and longer than daytime dives (Fig. 3.5). Both animals were tracked during subsequent migrations, and then displayed positive diel patterns of dive depth and duration. Dives rarely extended in depth to the seafloor (0.7% of all dives recorded reached depths within 25 m of the estimated bottom depth), and most dives were pelagic.

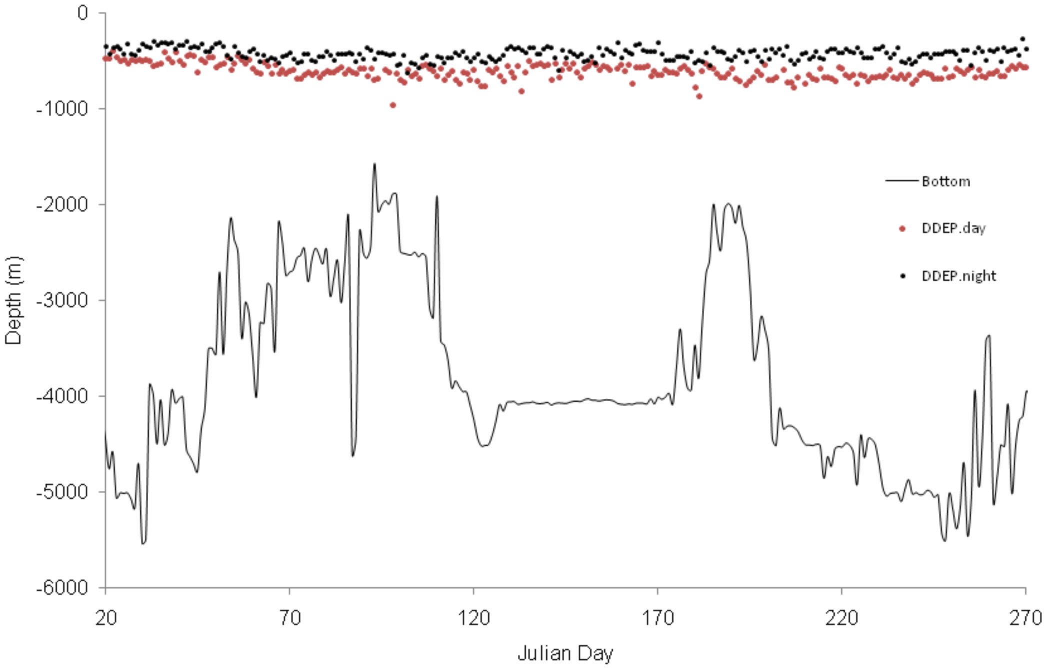

Figure 3.4: Time series plot indicating the average daytime (red dots) and night-time (black dots) dive depths of one track (OO371), illustrating positive diel variation. Estimated bottom depth is indicated by the solid black line.

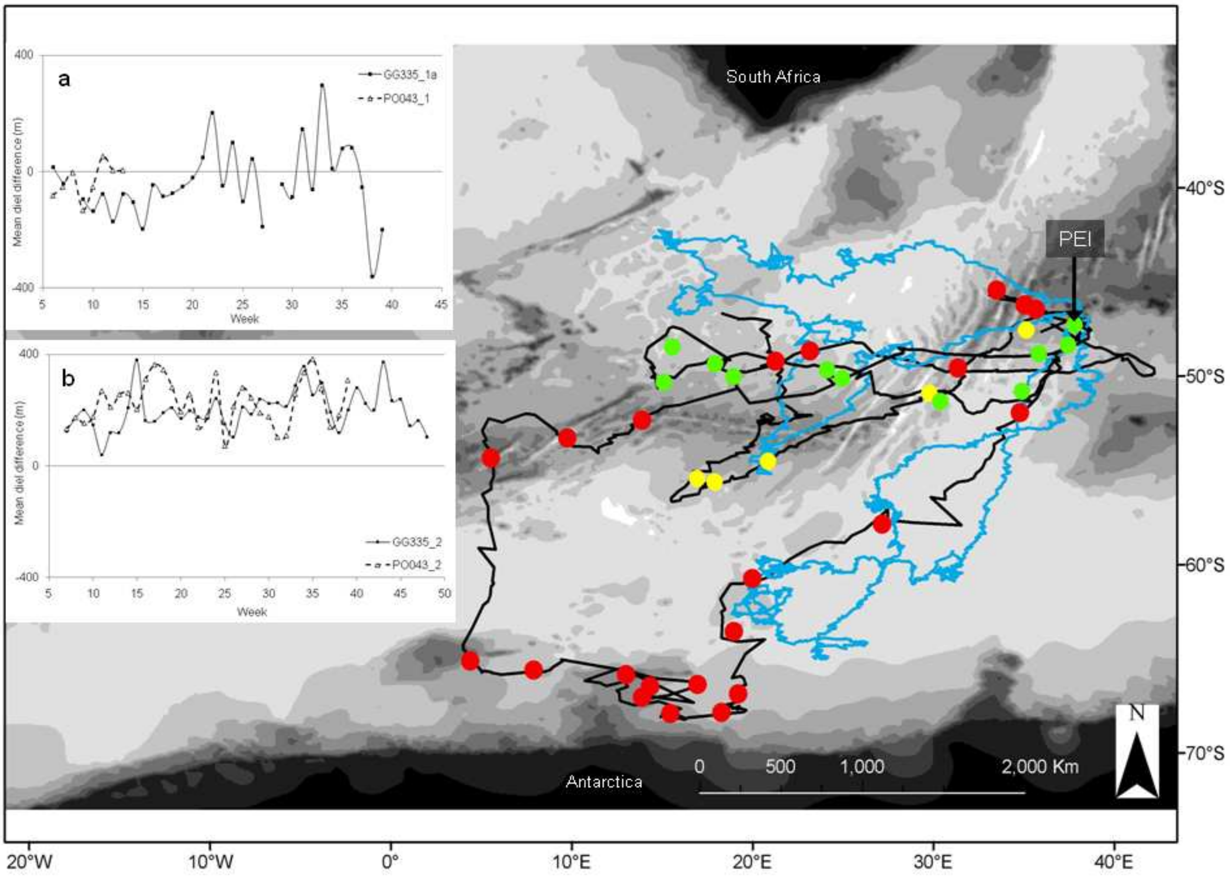

Figure 3.5: Map indicating movements of the two animals that displayed negative diel variation (deeper dives at night, than during the day. Colour-coded circles indicate areas where weekly averaged values of dive depths indicated negative diel variation during their 2007 migrations. Red = GG335_1a, Green = GG335_1b, Yellow = PO043_1. The 2008 migrations of both animals are indicated in blue. The inset time series plots indicate the weekly averaged differences in dive depths between daytime and night-time for (a) GG335_1a and PO043_1; and for (b) GG335_2 and PO043_2. Values below zero indicate negative diel variation, while values above zero indicate positive diel variation (deeper dives during the day, then at night).

Table 3.3: Summary dive statistics for individual tracks of southern elephant seal females. Values are reported as mean ± SD. Dep.Date = date of device deployment; Age = mean age during track period; Migr = migration stage (PM = post-moult; PB = post-breeding); SURF.DUR = surface duration; DIVE.DUR = dive duration; MAX.DEP = maximum dive depth.

Event	Track	Dep. Date	Age	Length	Migr	Days	Dives	SURF.DUR (min)		DIVE.DUR (min)		MAX.DEP (m)	
								DAY	NIGHT	DAY	NIGHT	DAY	NIGHT
M04af10	RG017	2004/04/15	10.6	NA	PM	44	1 140	2.3 ± 0.8	2.4 ± 1.1	37.1 ± 10.3	27.1 ± 9.3	680.9 ± 192.4	462.8 ± 176.3
M06sf01	YY189_1	2006/04/15	2.7	222	PM	161	4 036	2.3 ± 0.6	2.3 ± 0.7	34.9 ± 7	23.7 ± 6.5	638.3 ± 124.6	437.3 ± 128.1
M06sf02	YY096	2006/04/15	2.6	210	PM	28	885	2.2 ± 0.5	2.2 ± 0.6	32.6 ± 5.3	27 ± 6.6	506.1 ± 104.3	406 ± 121.1
M07af02a	YY189_2a	2007/02/01	3.6	224	PM	239	7 080	2.2 ± 0.8	2.2 ± 0.8	26.4 ± 10.4	20.8 ± 6.7	573.8 ± 156.9	429.8 ± 126
M07af02b	YY189_2b	2007/02/01	4.1	224	PB	57	2 100	2.2 ± 0.5	2.1 ± 0.3	20.4 ± 4.1	16.2 ± 2	614.4 ± 160.4	488.5 ± 146.5
M07af03a	GG335_1a	2007/01/30	7.6	NA	PM	222	1 244	2.2 ± 1	2.3 ± 1	31.1 ± 22.2	36 ± 20.1	406.4 ± 198.5	501.1 ± 210.3
M07af03b	GG335_1b	2007/01/30	8.1	NA	PB	61	613	2.7 ± 1.1	3 ± 1.4	16.9 ± 15.4	17.4 ± 15.8	280.7 ± 175.5	297 ± 222.3
M07af04	PO043_1	2007/01/31	8.4	254	PM	41	699	3.8 ± 2.7	4.5 ± 2.9	17.5 ± 17.4	19.7 ± 20.7	285.8 ± 161.2	290 ± 189
M07af06	OO021_1	2007/01/30	5.6	NA	PM	227	5 722	2.1 ± 0.7	2.1 ± 0.6	30.2 ± 9.3	25.6 ± 8.5	576.2 ± 148.2	399.6 ± 118.2
M07af16	OO371	2006/12/27	5.6	NA	PM	261	6 571	2.2 ± 0.5	2.3 ± 0.8	33 ± 11.1	27.4 ± 9.3	571.8 ± 142.3	414.7 ± 127.2
M07af17	YY240	2007/10/26	4.1	NA	PB	66	1 614	2.2 ± 0.6	1.9 ± 0.6	23.1 ± 5.4	15.1 ± 3.8	531.2 ± 163.1	300.4 ± 106.3
M07af18	YY193_1	2007/10/31	4.1	NA	PB	65	2 080	2.2 ± 0.7	2.1 ± 0.8	23.4 ± 6.9	15.2 ± 4.1	465.3 ± 128.5	309.5 ± 83.5
M07af19	YY070	2007/11/01	4.1	NA	PB	54	1 482	2.1 ± 0.5	1.9 ± 0.9	25.6 ± 6.5	16.8 ± 4.4	458.5 ± 119.1	321.9 ± 90.4
M07af20	YY348_1	2007/11/03	4.2	212	PB	69	1 750	2.4 ± 0.6	2 ± 1	25.4 ± 7.2	14.6 ± 6.5	525.1 ± 147.2	287.2 ± 104.7
M07af21	RR483	2007/11/03	3.1	213	PB	66	1 582	2.4 ± 0.8	2 ± 0.7	20.9 ± 6.1	14.6 ± 3.6	496.7 ± 146.5	320.6 ± 93.8
M07af22	YY264_1	2007/11/04	4.2	NA	PB	65	2 019	2.1 ± 0.7	2 ± 1.2	24.6 ± 5.9	16.7 ± 4.3	496.4 ± 121.3	323 ± 85
M08af07	OO021_2	2008/01/21	6.6	225	PM	226	5 313	2.2 ± 0.7	2.1 ± 0.6	33.4 ± 9.6	26.2 ± 9.1	564.8 ± 134.5	398.2 ± 112.9
M08af08	WW058	2008/01/21	7.6	244	PM	233	8 053	2.4 ± 0.9	2.2 ± 0.9	29.3 ± 10.1	24.9 ± 10.6	567 ± 198.2	379.4 ± 196.3
M08af09	WW061	2008/01/21	7.6	233	PM	235	6 299	2.3 ± 0.7	2.2 ± 0.6	32.8 ± 8.7	26.3 ± 8.4	608.4 ± 150.1	427.7 ± 148.2
M08af10	BB191	2008/01/26	5.4	217	PM	103	2 887	2.2 ± 0.7	2.4 ± 1.3	24.2 ± 8.9	23.2 ± 8.5	523.1 ± 153.9	395.1 ± 126

M08af11a	YY189_3a	2008/01/26	4.6	242	PM	243	6 589	2 ± 0.7	2.2 ± 0.9	29.4 ± 11.9	24.7 ± 9.2	545.4 ± 152.7	388.5 ± 121.5
M08af11b	YY189_3b	2008/01/26	5.1	242	PB	66	1 936	2.3 ± 0.6	2.3 ± 0.7	26.1 ± 6.4	18.9 ± 3	623.3 ± 164.5	519 ± 127.2
M08af12	PO043_2	2008/02/08	9.6	NA	PM	230	5 455	2.4 ± 0.8	2.3± 0.7	34.7 ± 13.4	23.7 ± 6.4	628.3 ± 177.3	421.1 ± 124
M08af13	YY193_2	2008/02/09	4.6	224	PM	180	5 849	2.1 ± 0.8	2.2 ± 1.1	29.1 ± 12.4	23.8 ± 12.6	510.1 ± 146.8	322 ± 162.7
M08af14	OO418	2008/02/09	6.5	230	PM	98	3 395	2.5 ± 0.5	2.2 ± 0.6	27.2 ± 8.1	22.2 ± 8.8	520 ± 173.4	379.3 ± 168.5
M08af15	GG335_2	2008/02/09	8.7	235	PM	293	8 510	2.3 ± 0.7	2.3 ± 1	35 ± 13.5	29.8 ± 12.7	601.5 ± 172.3	414.6 ± 175
M08af16	YY348_2	2008/02/12	4.6	227	PM	188	4 492	2.4 ± 0.7	2.3 ± 0.9	34.3 ± 13.4	21.7 ± 9	538.4 ± 208.2	360.8 ± 184.1
M08af17	YY039	2008/02/19	4.6	216	PM	169	4 740	2 ± 0.5	2 ± 0.5	28.4 ± 12.1	23.9 ± 8.3	479.3 ± 167.4	390.3 ± 121.6
M08af18	YY264_2	2008/02/19	4.5	236	PM	160	4 422	2.1 ± 0.7	2 ± 1.2	31.6 ± 11.8	24.1 ± 9.7	532.7 ± 151.4	310.6 ± 138.2
M08af21	GG380	2008/11/05	9.1	NA	PB	17	445	2.2 ± 0.5	2.2 ± 1	22 ± 2.9	17.3 ± 3.9	487 ± 76.5	339 ± 101.6

Dive types

U-shaped and wiggle (W) dives were the most commonly identified dive types. U-shaped dives accounted for 65.1% of all dives recorded and W dives for 30.6%. The remaining dive types accounted for less than 5% of the dives recorded (DR = 0.9%, R = 0.9%, SQ = 0.7%, V = 1.8%). The distributions of dive types were similar between migrations. Differences were observed in the frequency of occurrence of U-shaped dives between day stages, with more U-shaped dives undertaken during daytime, when compared to night-time ($X^2 = 31.2$, df = 1, $p < 0.001$). The frequency of W dives showed an inverse relationship to that of U-shaped dives, with more W dives recorded at night than during the day ($X^2 = 6410.8$, df = 1, $p < 0.001$).

The various dive types were carried out in water of similar seafloor depth estimates (Table 3.4), though a statistically significant difference between the dive types was detected ($F_{5,\ 108883} = 12.4$, $p < 0.001$). Post-hoc Tukey test outputs revealed that significant differences existed in the seafloor depth estimates between V- and SQ dives, between V- and U dives, and between W- and U dives.

Table 3.4: Mean estimates of seafloor depths for locations where animal exhibited various dive types. W = wiggle dives; U = U-shaped dives; SQ = square dives; DR = drift dives; V = V-shaped dives; R = root dives.

Dive type	Seafloor depth (m) (mean ± SD)
W	4 335 ± 907
U	4 291 ± 965
SQ	4 242 ± 1012
DR	4 266 ± 953
V	4 367 ± 958
R	4 289 ± 934

Forage effort dives

Forage effort dives during post-breeding migrations were concentrated in the western portions of the total area utilised by the tracked elephant seals (Figs. 3.6 and 3.7). Daytime forage effort dives were largely restricted to areas west of the Andrew Bain fracture zone (ABFZ) (~ 30°E), while night-time forage effort dives were less concentrated throughout the utilised area and also occurred east of the ABFZ. Both day- and night-time forage effort dives were less common in immediate proximity to Marion Island (within a radius of ~ 250 km to

Marion Island). The ratio of forage effort dives showed a weak positive, but statistically significant, correlation with distance from Marion Island (Day: $r = 0.36$; df = 544; $p < 0.001$, Night: $r = 0.4$; df = 509; $p < 0.001$).

Forage effort dives during post-moult migrations were also concentrated to the west of the ABFZ (Figs. 3.8 and 3.9). Day- and night-time forage effort dives occurred north and south of the South-West Indian Ridge (SWIR). Few localities appeared to have high concentrations of forage effort dives recorded during both day and night periods. One area where both day- and night-time forage effort dives appeared to be concentrated was situated on the southern boundary of the ABFZ (~ 25°E; 55°S). Both day- and night-time forage effort dives appeared to also be concentrated in an area of approximately 3 160 km^2 situated at ~ 1°E; 61°S. No concentrations of forage effort dives were evident in close proximity to the Antarctic continental shelf. The ratio of forage effort dives showed a weak, positive correlation with distance from Marion Island (Day: $r = 0.12$; df = 3219; $p < 0.001$, Night: $r = 0.12$; df = 3197; $p < 0.001$).

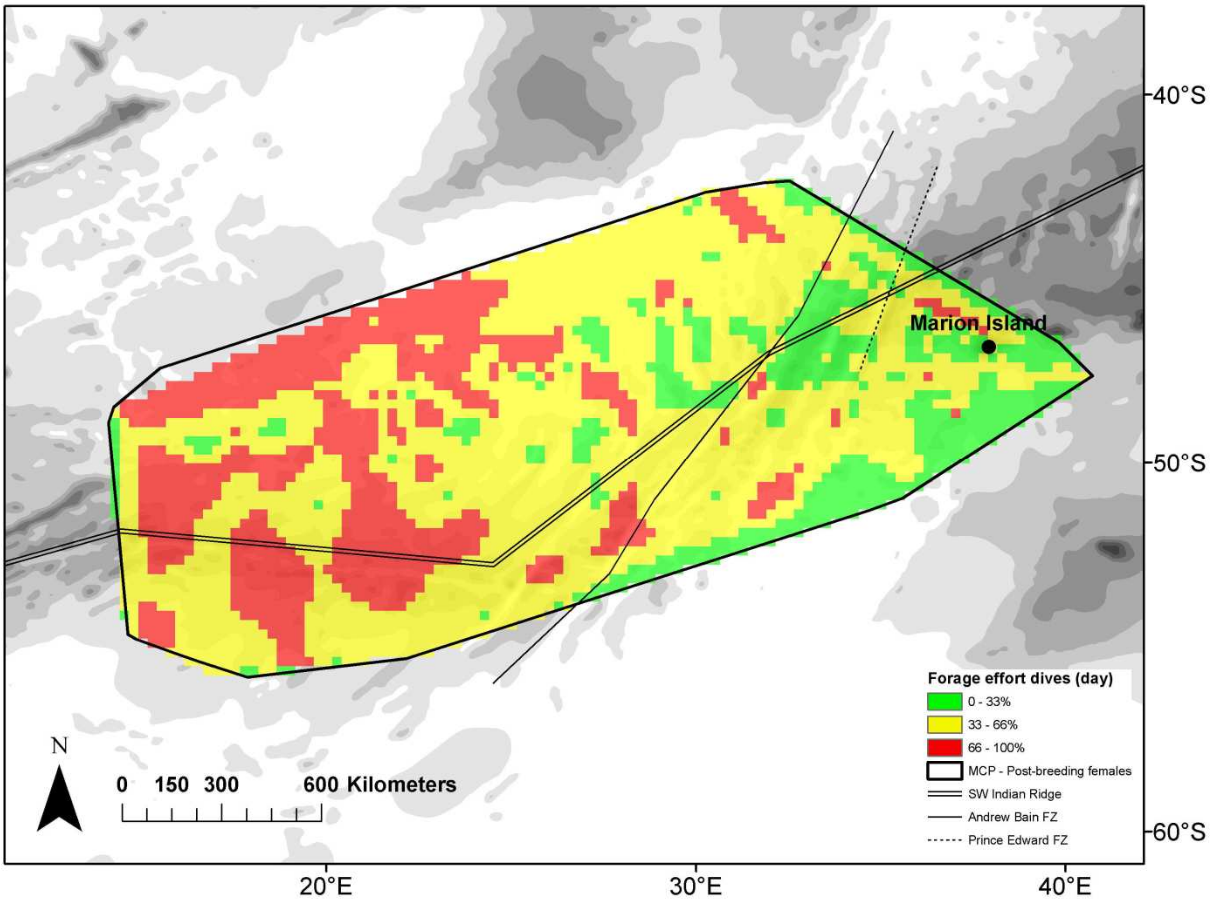

Figure 3.6: Map indicating daytime ratios of forage effort per day (ratio of U-shaped dives, with greater-than-expected bottom times) for the area utilised by female southern elephant seals during post-breeding migrations. Positions of prominent bathymetric features are also indicated (Southwest Indian Ridge, Andrew Bain Fracture Zone and Prince Edward Fracture Zone).

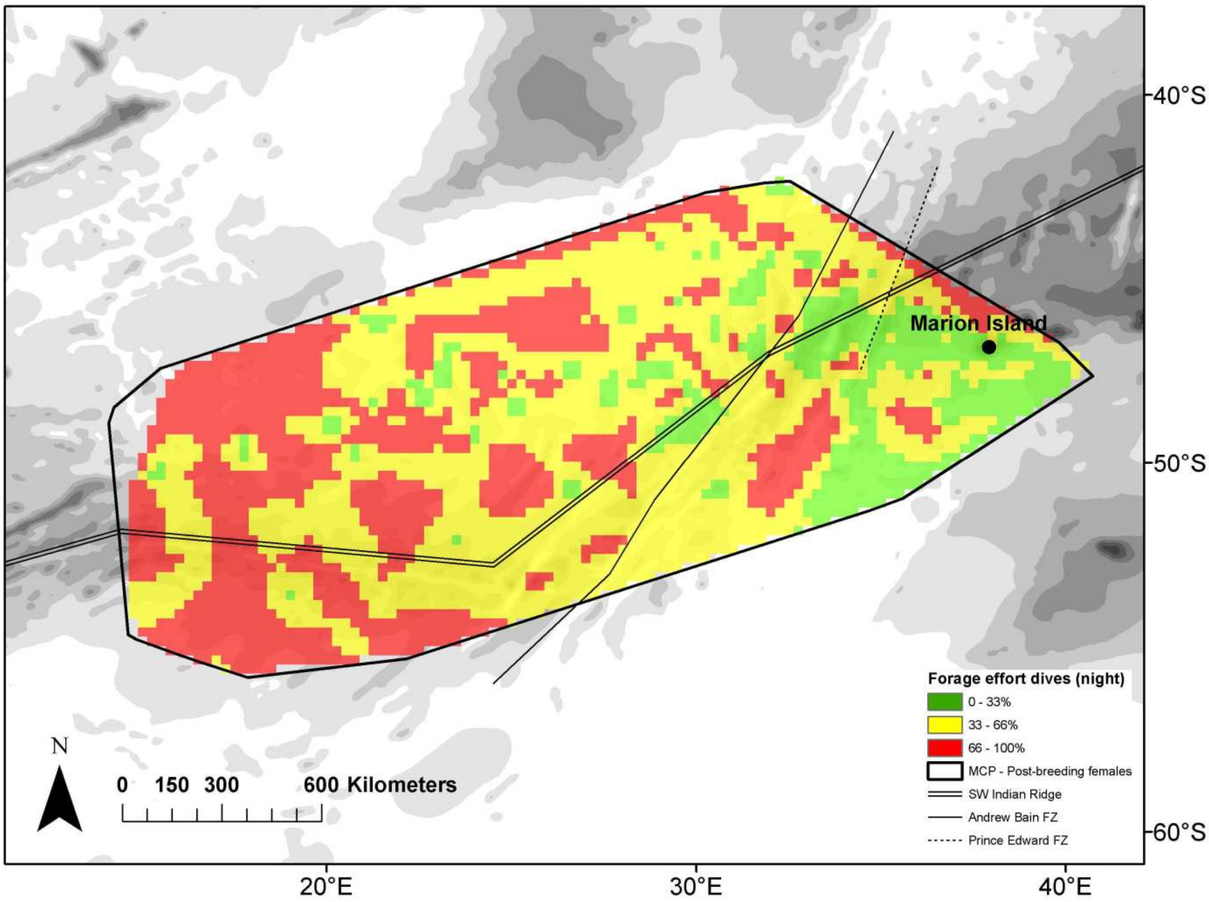

Figure 3.7: Map indicating night-time ratios of forage effort per day (ratio of U-shaped dives, with greater-than-expected bottom times) for the area utilised by female southern elephant seals during post-breeding migrations. Bathymetric features are the same as for Fig. 3.6.

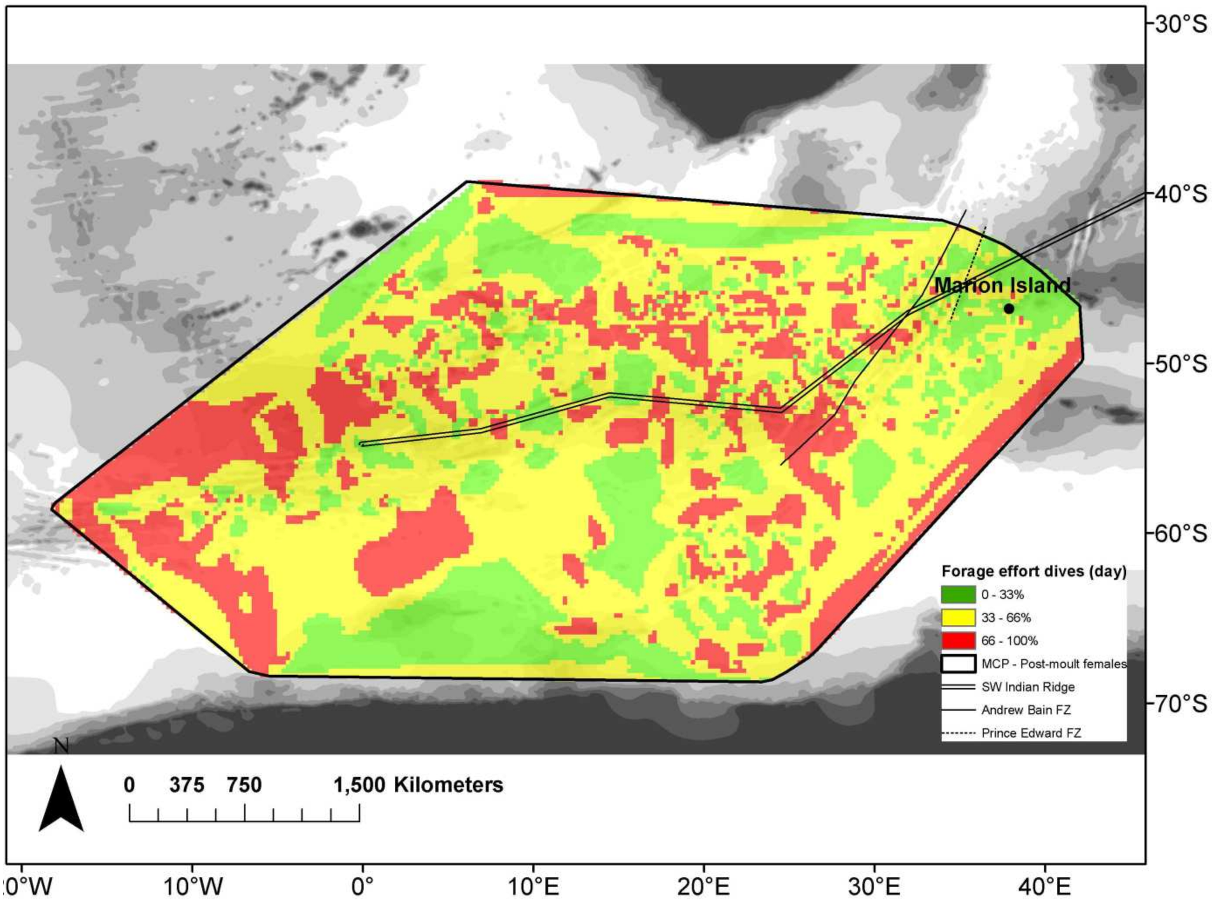

Figure 3.8: Map indicating daytime ratios of forage effort per day (ratio of U-shaped dives, with greater-than-expected bottom times) for the area utilised by female southern elephant seals during post-moult migrations. Bathymetric features are the same as for Fig. 3.6.

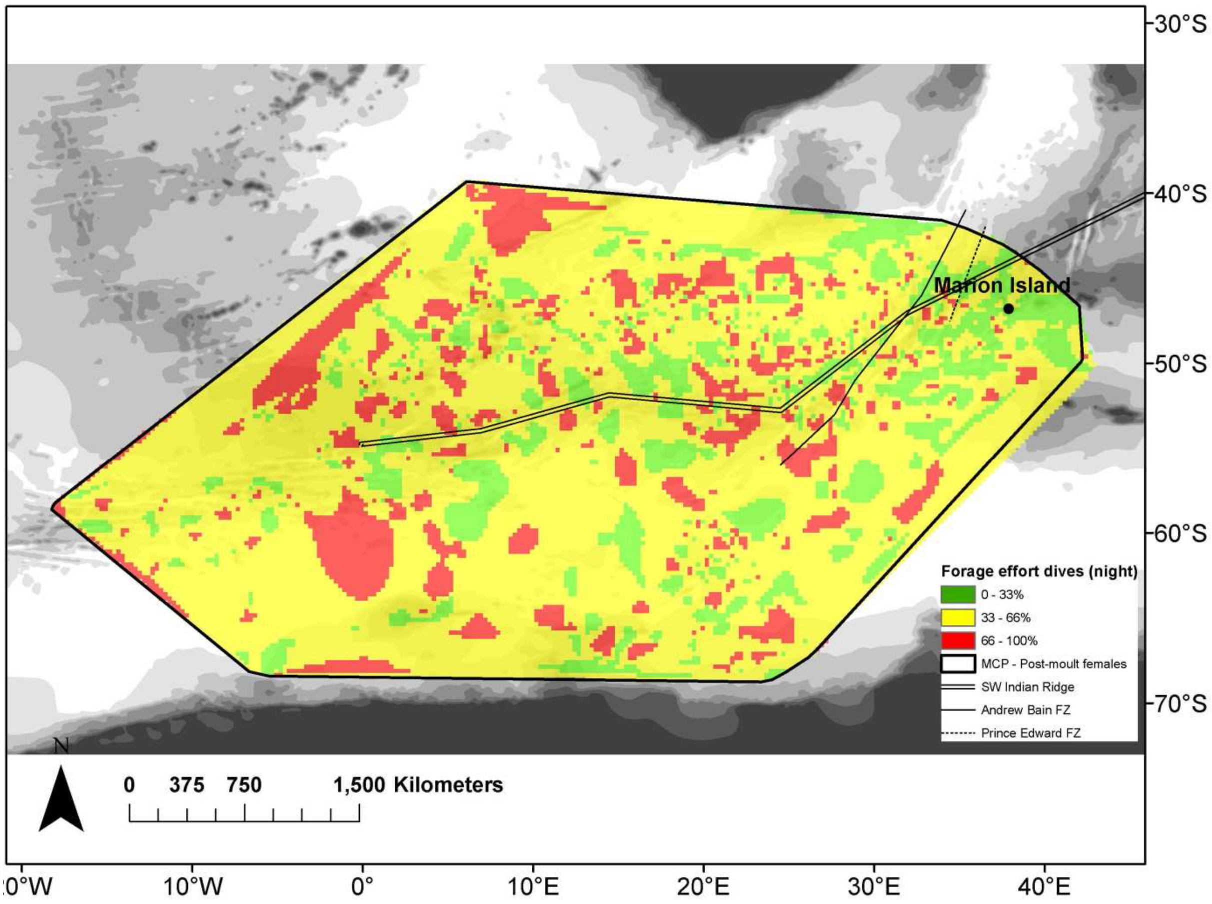

Figure 3.9: Map indicating night-time ratios of forage effort per day (ratio of U-shaped dives, with greater-than-expected bottom times) for the area utilised by female southern elephant seals during post-moult migrations. Bathymetric features are the same as for Fig. 3.6.

Discussion

Female southern elephant seals from Marion Island undertake relatively predictable foraging migrations, largely travelling in south-western directions away from the island (Tosh 2010). This study describes the water depth usage by females from this population between 2004 and 2008.

Dive depths and durations

Our results indicate that females from Marion Island tend to follow a similar strategy to females from other populations and forage pelagically, displaying positive diurnal variation in dive depths and durations (Hindell et al. 1991; Campagna et al. 1995). Female southern elephant seals tagged at Macquarie Island dived to mean depths of approximately 395 m during post-moult migrations, and between 419 and 453 m during post-breeding migrations – such dives lasting for a mean period of 27.1 min during post-moult migrations, and 21.1 min during post-breeding migrations (Hindell et al. 1991; Field et al. 2001). Female southern elephant seals from the Kerguelen archipelago dive to mean pelagic depths that range between 249 and 487 m, lasting for mean periods of between 13.6 and 30.9 min (Bailleul et al. 2007a). Similarly, females from Peninsula Valdés display diel variation and dive to mean depths of 431 m for periods of approximately 22.8 min (Campagna et al. 1995).

Mean dive depths and durations reported in our study compare well with previous investigations into the dive behaviour of female southern elephant seals at Marion Island (Jonker & Bester 1994). However, female elephant seals from Marion Island tend to undertake slightly deeper and longer dives during post-moult migrations, when compared to females from other populations (Post-moult: $\text{Dive.Dep}_{\text{DAY}}$ = 560 m; $\text{Dive.Dep}_{\text{NIGHT}}$ = 394 m; $\text{Dive.Dur}_{\text{DAY}}$ = 30.9 min; $\text{Dive.Dur}_{\text{NIGHT}}$ = 24.9 min). Further, Marion Island females tend to dive deeper (but for similar durations) during post-breeding migrations, when compared to reported results from other populations (Post-breeding: $\text{Dive.Dep}_{\text{DAY}}$ = 517 m; $\text{Dive.Dep}_{\text{NIGHT}}$ = 359 m; $\text{Dive.Dur}_{\text{DAY}}$ = 23.3 min; $\text{Dive.Dur}_{\text{NIGHT}}$ = 16.1 min). Such values suggest that females from Marion Island may be operating closer to their physiological limit when foraging at sea, when compared to females from other populations (Hindell et al. 2000). This may result in the Marion Island elephant seals being more vulnerable to changes in the availability of prey or the location thereof if such changes would require them to forage at increased water depths.

Dive types

The prevalence of U-shaped dives in our sample suggests probable foraging activity in pelagic environments. U-shaped dives were more common during daytime dives, when compared to night-time dives during both post-breeding and post-moult migrations. Superficially this suggests that proportionally more foraging activity is undertaken during daytime dives. However, wiggle dives were the next most abundant dive type in our sample and displayed the opposite pattern between day- and night-time dives (more common at night, compared to during the day). These dives may also serve a foraging purpose and our results rather suggest a possible difference in strategy between day- and night-time dives. The prevalence of wiggle dives at night may also be the result of the night-time dives being shallower as a result of vertical migration of prey (Hays 2003; Collins & Rodhouse 2006; Collins et al. 2008). Seals may therefore have more time at preferred depths before surfacing to breathe. This may allow them more flexibility in changing their depths in pursuit of prey during such dives, resulting in a wiggle pattern.

V-shaped dives, suggesting exploratory activity, were uncommon in our sample, comparing well with results obtained from animals tagged at South Georgia (Photopoulos 2007). Such dives are presumably physiologically costly to the animal, since no foraging activity is associated with it and they often extend to relatively increased depths, with fast descent and ascent rates (presumably requiring substantial energetic expenditure). These dives were more common in our sample in deeper water (4 367 ± 958 m) than other dive types. Though this difference was statistically significant, the differences between bottom depth estimates for the various dive types were generally small and likely to not be biologically very informative. SQ (square) dives are thought to result from benthic foraging (Photopoulos 2007). These were predictably rare in our sample, since very few recorded dives extended to the vicinity of the seafloor. The SQ dives identified in our sample were typically still in waters with seafloor depths considered to be out of reach of our study animals (4 242 ± 1012 m). Photopoulos (2007) reported the identification of approximately 3% of all dives recorded in adult male and female southern elephant seals from South Georgia as DR (drift) dives. Our results identified a smaller proportion of dives in our sample as DR dives (0.9%). Such dives are associated with rest in elephant seals (Biuw et al. 2003; Mitani et al. 2009). The drift rate of an animal (vertical rate of depth change in DR dives) is directly influenced by its buoyancy, which in turn is affected by the blubber thickness. Since blubber thickness is associated with forage success, the drift rates of DR dives has been employed as indicators of forage success in elephant seals (Biuw et al. 2003; Bailleul et al. 2007b; Biuw et al. 2007; Robinson et al. 2010). The rarity of DR dives in our sample precluded the use of this measure of forage success. This comparative rarity of DR dives in our sample was considered unlikely to be the result of differences in rest behaviour between Marion Island elephant seals and other populations. Rather, the lack of DR dives may be an unintentional result of the broken-stick compression algorithm onboard some SRDLs, resulting in slight differences in inflection point estimates (Biuw pers.comm.). A proportion of the actual DR dives undertaken by our study animals were therefore likely identified as either U- or W-shaped dives. The function of R (root) dives is unclear. These dive types were also rare in our sample and further investigation into their potential role is required.

Areas of forage effort

We characterised areas utilised by female southern elephant seals within the Southern Ocean according to the relative amounts of "forage effort" of the tracked animals displayed through the dominant dive type (U-shaped dives). The maps generated by plotting ratios of high forage effort dives within the areas utilised, indicate that female southern elephant seals tend not to undertake high effort dives in close proximity to Marion Island. While high forage effort dives showed a large amount of scatter throughout the plots, the (weak) positive correlations between forage effort dives and distance from Marion Island indicate that females likely forage less at the beginnings and ends of migrations. Forage effort dives were not absent during these stages however, and females almost certainly forage opportunistically then. The presence of high forage effort dives throughout the ranges of the females in this sample indicates a general strategy of moving continuously in search of pelagic prey and agrees with previously published results on the dive behaviour of southern elephant seal females tagged at Peninsula Valdés (Campagna et al. 1995), South Georgia (Boyd & Arnbom 1991) and Macquarie Island (Hindell et al. 1991; Slip et al. 1994). However, the general lack of areas of high forage effort close to the Antarctic shelf area is different from recorded behaviour for female southern elephant seals from the Kerguelen Islands (Bailleul et al. 2007a) and Macquarie Island (Hindell et al. 1991). This is most likely related to the greater distance that Marion Island is situated from the Antarctic continental shelf, making it more costly for animals from this population to travel as far south. This may be indicative of inter-population differences in diet of female southern elephant seals, but requires more investigation into the diet of animals from Marion Island in particular.

While these results do provide broad-scale indications of the spatial distribution of forage effort in the tagged animals from Marion Island, detailed interpretations should be made with caution. Unequal sampling throughout the areas of use (minimum convex polygons) is likely to have resulted in some bias being introduced by the interpolation methods followed here.

For instance, the dive effort map of post-breeding females indicates concentrations of high effort dives taking place along the north-eastern boundary of the MCP (Fig. 3.6), though very few data points were recorded in that area (Fig. 3.2). Similarly, the dive effort map of post-moult females also indicates some areas of high forage effort (notably along the south-eastern boundary of the MCP), where little dive activity actually took place. Further, our sample size did not allow for useful inter-annual comparisons of dive effort areas at a scale representative of the population. It is likely that some variation exists between years, introducing some bias into our results. Nonetheless, when viewing the track data (Figs. 3.2 and 3.3) and the "forage effort" maps (Figs. 3.6-3.9) in conjunction, it is evident that concentrated areas of high forage effort occur outside of a radius of approximately 215 km from Marion Island for post-breeding tracks, and similarly outside a radius of approximately 245 km from the island for post-moult tracks.

Forage strategy

Southern elephant seals are thought to broadly adopt one of two foraging strategies, either foraging pelagically after vertically migrating prey or foraging benthically on bottom-dwelling prey (or some combination thereof) (Hindell et al. 1991; Jonker & Bester 1994; Le Boeuf & Laws 1994b; Bennet et al. 2001; Campagna et al. 2007). Recently Biuw et al. (2010) described the evident plasticity in forage strategy of southern elephant seals from Bouvetøya. They reported that animals switched between forage strategies depending on the hydrographic regime or seasonal environmental conditions of areas they were travelling through. Elephant seals from that investigation switched between pelagic strategies that involved diel vertical migration (pelagic, ice-free environments) to benthic strategies (on the Antarctic continental shelf) and pelagic strategies without diel vertical migration (pelagic areas covered by winter sea ice). Female elephant seals from Marion Island evidently do not travel to the Antarctic continental shelf very often and restrict their movements mostly to areas that remain ice free in winter months (this study). Vertical diel variation of zooplankton is common throughout the world's oceans, resulting in similar patterns of diel variation in higher trophic levels that include fish, marine mammals, reptiles and birds (Hays 2003). Since many pelagic prey species of elephant seals exhibit positive diel variation (Collins & Rodhouse 2006; Collins et al. 2008), it is not surprising that females in our study mostly displayed a similar vertical diel pattern and evidently targeted vertically migrating prey species.

One animal (GG335) displayed periods of a negative diel diving pattern throughout two migrations (2007 post-moult and post-breeding), then switched to a positive diel variation diving pattern during her 2008 post-moult migration. During her 2007 post-moult migration GG335 travelled far south up to the Antarctic continental shelf. During the post-breeding migration of the same year, GG335 travelled west of Marion Island and did not go further south than approximately 53°S. During the 2008 post-moult migration she again travelled relatively far south, but stayed north of approximately 66°S. PO043 also displayed a negative diel variation pattern during the first part of her 2007 post-moult migration – early device failure during this migration precluded obtaining further data. She also switched to a positive diel variation strategy during her subsequent 2008 post-moult migration. The positions of areas where both these animals displayed negative diel vertical migration were spread across various localities of varying depths and oceanographic conditions. It is difficult to speculate on the potential prey being targeted by southern elephant seals when they display negative diel variation in dive depths. Since neither day- or night-time dives extended to the seafloor when animals were displaying negative diel variation, it is possible that this may present a third type of foraging strategy in southern elephant seals. Previously, Jonker (1997) reported on a female elephant seal tracked from Marion Island that switched from a positive to a negative diel variation pattern of diving upon reaching Antarctic ice-shelf water. He postulated that the animal switched to a diet of Antarctic silverfish (*Pleuragramma antarcticum*) during this phase. Both animals in our study displayed negative diel variation also in areas free of sea-ice, making this behaviour difficult to explain. Unfortunately, the temperature probes on both devices carried by GG335_1 and PO043_1 failed prematurely, precluding assessments of the *in situ* hydrographic properties of the water masses in which they displayed negative diel vertical migration. Continued at-sea monitoring of the movements and dive behaviour of Marion Island elephant seals and the linking of such behaviour with oceanographic conditions, as well as dietary investigations will help to clarify this behaviour.

Conclusion

Dive data recorded for female southern elephant seals tagged at Marion Island indicated largely pelagic feeding on vertically migrating prey. This strategy is similar to those described for other populations of this species, though dive depths obtained by Marion Island females tended to be deeper than those recorded for females from other populations. No animals appeared to forage benthically and some displayed negative diel variation in dive depths (diving deeper at night, than during the day). Areas of high forage effort were distributed throughout their ranges, indicating opportunistic foraging throughout their migrations, though comparatively little foraging took place in close proximity to Marion Island.

CHAPTER FOUR: WATER COLUMN USE AND FORAGE STRATEGIES OF MALE SOUTHERN ELEPHANT SEALS FROM MARION ISLAND*

Abstract

We describe the water column use of 9 adult and 13 subadult male southern elephant seals (*Mirounga leonina*) satellite tagged at Marion Island between April 2004 and November 2008. Animals mostly foraged pelagically where much variation was evident in forage strategies, with seals sometime exhibiting positive diel vertical migration (diving deeper during the day, compared to night-time) and at other times the reverse. Adult males tended to stay in closer proximity to Marion Island than subadult males. Areas of increased forage effort were varied and distributed throughout the areas utilised by males. While a few such areas of increased forage effort appeared to be associated with seafloor ridges and fracture zones, no statistical relationships were evident between forage effort and seafloor depth. No significant differences were recorded for dive durations or dive depths between adults and subadults. However, younger animals (< 6 yrs) displayed a positive relationship between dive durations and age, as well as between dive depths and age, while these relationships disappeared for older animals between the ages of 6 and 14. Our results indicate that male elephant seals exhibit much variability in dive strategy and are seemingly capable of exploiting a range of different prey types occurring in various depth layers.

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*Submitted for publication as: McIntyre, T., Bornemann, H., Plötz, J., Tosh, C.A. & Bester, M.N. (under review) Water column use and forage strategies of male southern elephant seals from Marion Island. *Aquatic Biology*

Introduction

Differences in forage strategy between juveniles and conspecific adult animals are relatively common in vertebrates (Diamond & Bond 1991; Fowler et al. 2006; Graham et al. 2007). Reasons for such differences are varied and include differences in dietary requirements (Sullivan 1988; Cardona et al. 2010), morphological and physiological capacity (Ponganis et al. 1999; Barbini et al. 2010; Lea et al. 2010), and experience (Heinsohn 1991; Langen 1996; Ishii & Shimada 2010) between younger and older animals. In marine mammals foraging strategies are often dependent on the body sizes of individuals and the concomitant physiological capacity associated with it (Hindell et al. 2000; Irvine et al. 2000). Larger animals are likely to be able to dive to deeper depths and remain at such depths for longer periods to exploit prey species occurring there, though some reports have suggested that some age-related dietary changes in seals depend on age-related learning (Drago et al. 2009).

There are relatively few reports describing the dive behaviour of male (particularly adult) southern elephant seals (*Mirounga leonina*), when compared to the numerous reports on female and juvenile animals (e.g. Jonker & Bester 1998; Bennet et al. 2001; Field et al. 2001; Bailleul et al. 2007a). The existing reports do however suggest that male seals tend to target shelf areas and/or shelf edges, where they mostly forage benthically at relatively shallow depths (Hindell et al. 1991; Campagna et al. 1999; Biuw et al. 2010). This is in contrast to female elephant seals that mostly forage pelagically over deeper waters (Campagna et al. 1995; Bornemann et al. 2000; chapter 3). Dietary studies of southern elephant seals have indicated predominant foraging on cephalopods and myctophid fish (Rodhouse et al. 1992; Daneri et al. 2000; Daneri & Carlini 2002; Lewis et al. 2006; Cherel et al. 2008), though little is known about the diets of elephant seals at a prey species level. The diet of southern elephant seals at Marion Island is also poorly known, and inter-population differences in dive- and migration behaviour suggest likely differences in diet in this population when compared to others (chapter 3).

Marion Island (46° 54’S; 37° 45’E) is one of two islands collectively forming the Prince Edward Islands and is situated in the southern Indian Ocean. The southern elephant seal population here forms one of the northernmost breeding aggregations in this species. This location is relatively far away from any continental shelves and other areas of relatively shallow bathymetry, as well as the Antarctic ice edge. Movement data from this population has provided evidence for a dependence in this population on the complex interactions of water movements associated with the Antarctic Circumpolar Current (ACC) and the Southwest Indian Ridge (SWIR), particularly at fracture zones, such as the Andrew Bain Fracture Zone (ABFZ) (Tosh 2010). The only previous investigation into the dive behaviour of male elephant seals from this population showed that animals mostly dived pelagically within relatively close proximity to Marion Island (~ 1 200 km) (Malherbe 1998). More recent investigations into the movements of males from Marion Island has revealed much variability in distances covered, with some animals remaining very close to the island (~ 20km), but a few others moving distances of more than 2 300 km from the island (Tosh 2010).

Here we describe the water column usage by adult and subadult male southern elephant seals from Marion Island. We identify areas of increased forage effort using a method whereby we assess the relative amounts of time spent near the deepest parts of dives for specific dive types believed to have a foraging purpose. We further describe differences in diel vertical migration strategy observed for animals from this population.

Methods

We deployed 24 satellite-relay data loggers (SRDLs) (Sea Mammal Research Unit, University of St. Andrews, Scotland) on subadult and adult male southern elephant seals hauled out at Marion Island between April 2004 and November 2008. All deployments, except for one, were on males of known age and birth-site that were flipper-tagged after weaning on the island (Bester 1988b). Series 9000 SRDLs and CTD-SRDLs were used in this investigation. Deployment details are as described in chapter 3. All dive-, track-, temperature and associated meta-data are available via the PANGAEA information system (http://pangaea.de).

Tracks

Track data were filtered based on assumed maximum swim speeds and turning angles (Freitas et al. 2008) as detailed in chapter 3 . Filtered plots were illustrated in ArcGIS 9.2 (ESRI, Inc.). Minimum convex polygons (MCPs) of combined tracks for different age classes (adults and subadults) were calculated using Hawth's Analysis Tools (Version 3.27 © 2002-2006). Animals older than 6 yrs of age, the age at which they first control female groupings (harems) during the breeding season (Pistorius et al. 2005) at or after a secondary growth spurt in their fourth to sixth year (Carrick et al. 1962; Ling & Bryden 1981) were assumed to be adults, and animals younger than 6 yrs subadults.

Dives

Individual dives were labelled as having either occurred during the day or at night (excluding periods within 30 min of the local sunrise and sunset times), based on local time values and local times of sunrise and sunset, calculated using the 'maptools' package (Lewin-Koh & Bivand 2008) in the R environment (R Development Core Team 2008).

We calculated relative proportions of time spent by animals during the bottom phase of U-shaped dives, as a modification of a method first presented by Bailleul et al. (2008) to identify areas of increased forage effort. This is described in detail in chapter 3. Briefly, we classified dives as being one of six predefined dive types, based on their time-depth profiles. Dive types identified included U-shaped (U), V-shaped (V), square (SQ), drift (DR), wiggle (W) and root (R) dives. After manually classifying a subset of dives, we used Breiman's random forest algorithm to classify remaining dives based on a total of 18 variables calculated for each dive (Photopoulos 2007). U-shaped dives for each track (separated by day and night) were extracted from the dataset, before being subjected to a linear regression to quantify the relationship between maximum dive depth, dive duration and time spent within the deepest 20% of each dive (bottom time). Residuals from the regression were then used to identify dives of increased 'forage effort', based on above-average amounts of time spent at the bottoms of dives.

Seafloor depth estimates were extracted from the GEBCO Digital Atlas, GDA, (IOC et al. 2003) for daily averaged location estimates for each track. We calculated daily averaged dive parameters (day and night separately) for each track. These parameters included: mean surface times ($\text{Surf.Dur}_{\text{DAY}}$ and $\text{Surf.Dur}_{\text{NIGHT}}$), mean dive durations ($\text{Dive.Dur}_{\text{DAY}}$ and $\text{Dive.Dur}_{\text{NIGHT}}$) and mean dive depths ($\text{Dive.Dep}_{\text{DAY}}$ and $\text{Dive.Dep}_{\text{NIGHT}}$). We also calculated the ratio of U-shaped dives with positive bottom time residuals (rUBT_{DAY} and $\text{rUBT}_{\text{NIGHT}}$) as an indicator of forage effort. We further attributed each seal day as exhibiting either a positive diel vertical strategy (DVS) (if the mean ± SE of day-time dive depths exceeded the mean ± SE of night-time dive depths by more than 25 m), negative DVS (reverse of positive diel variation) or neutral DVS (where the differences in mean ± SE of dive depths were less than 25 m between day and night). A cut-off value of 25 m was chosen as representing a value of approximately 5% of the mean dive depths of southern elephant seals from this population (chapter 2).

rUBT were mapped for different age-classes (subadult and adult), where animals older than 6 yrs were assumed to be adults, and animals younger than 6 yrs subadults. We used nearest neighbour interpolation in ArcMap 9.2 (ESRI, Inc) to generate raster outputs of rUBT within each MCP at a 0.25° grid scale. These were then presented after applying a mask, based on percent volume contours generated using Hawth’s Analysis Tools (Version 3.27 © 2002-2006). Dive analyses were undertaken in the R environment (R Development Core Team 2008), as well as Microsoft Office Excel ® 2007. Unless otherwise stated, mean values ± SD are reported. Statistical significance was set at $p \leq 0.05$.

Results

Data were retained from 22 tracks after two SRDLs failed prematurely and did not return usable dive data for this investigation. Tracks lasted for a mean period of 158 days (range: 61 – 300). Subadult males were a mean age of 4.1 (range: 1.8 – 5.8) yrs at the time of deployment, while adult males were a mean age of 8.9 (range: 6.6 – 13.6) yrs at the time of deployment.

Tracks

Adult males travelled in a predominantly westerly direction from Marion Island during their forage migrations (Fig. 4.1). Two animals travelled to areas north of the Subantarctic

Front (SAF), while the remaining animals either stayed in close proximity to the island, or travelled in a south-westerly direction in closer proximity to the SWIR. Subadult males mostly travelled in similar directions as adult males, with some animals travelling directly west and north-west of the island to areas north of the SAF, and others travelling in a south-westerly direction south of the SWIR (Fig. 4.2). Two subadult males travelled further south than 65°S and reached areas in close proximity to the Antarctic continental shelf, while one animal in our sample travelled in an easterly direction and reached Iles Crozet. There was much variability in distances travelled from the island in animals from both age-classes, though subadult males travelled further mean distances from the island (1 400 ± 1 173 km) than adult males (860 ± 660 km).

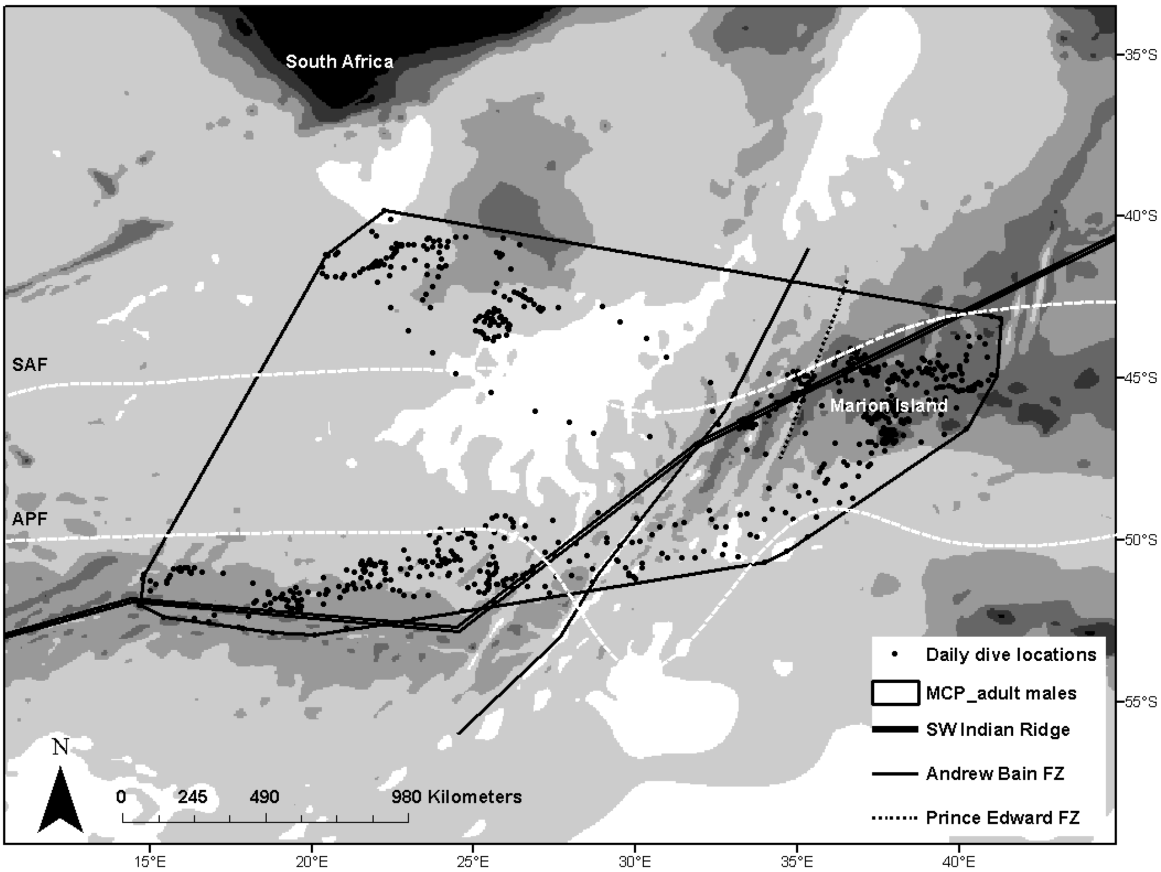

Figure 4.1: Map indicating plots of daily averaged position estimates obtained from adult male southern elephant seals tracked from Marion Island. A minimum convex polygon (MCP) indicates the area of utilisation. Approximate positions of the Antarctic Polar Front (APF) and Subantarctic Front (SAF) are indicated (from Belkin & Gordon 1996).

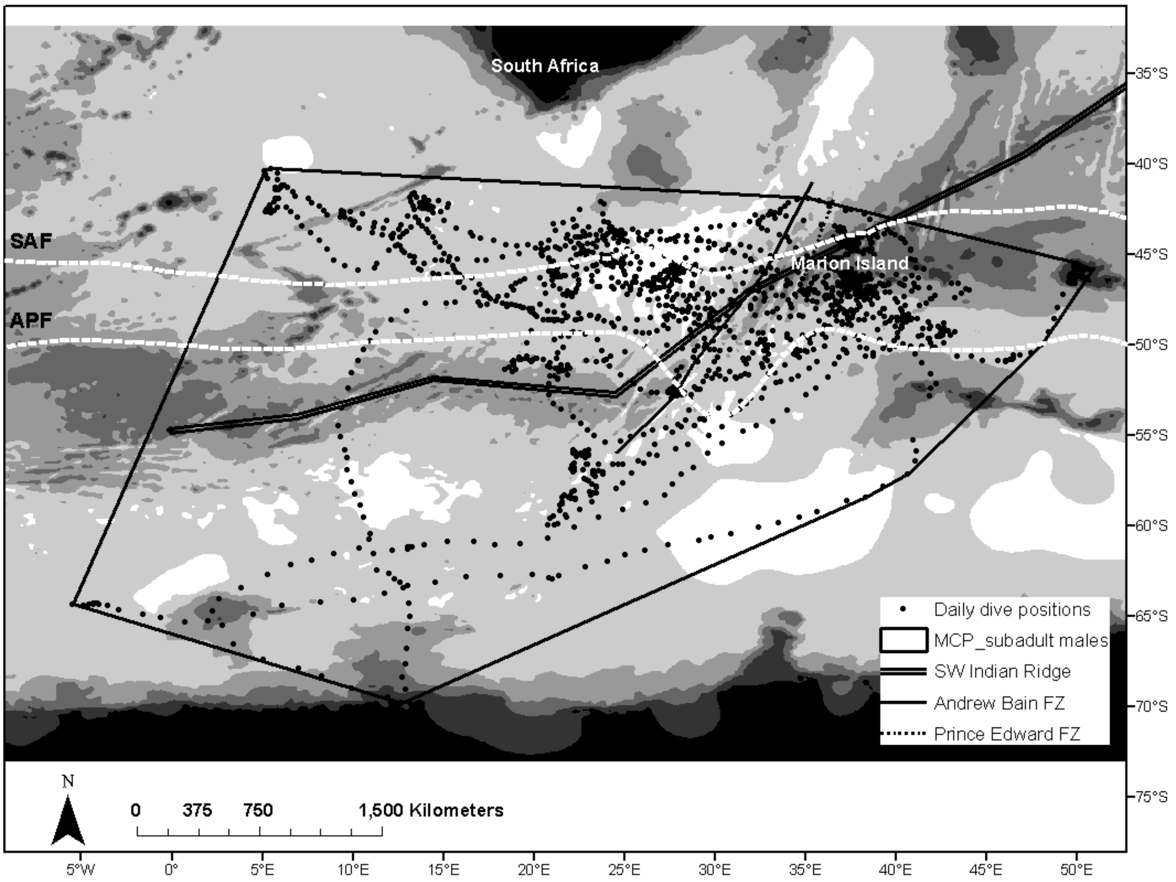

Figure 4.2: Map indicating plots of daily averaged position estimates obtained from subadult male southern elephant seals tracked from Marion Island. A minimum convex polygon (MCP) indicates the area of utilisation. Frontal positions are the same as for Fig. 4.1.

Dive behaviour

Uplinks resulted in the successful recording of 63 925 dive profiles, over 3 310 seal track-days. Tracks lasted for a mean period of 157.8 ± 67.2 days and contained 2 906 ± 1 692 transmitted dive profiles. Subadult males dived to similar day- and night-time depths as adult males (Table 4.1) and no significant differences were evident in dive durations (Wilcoxon signed rank test - Day W = 63.5, p = 0.76; Night W = 76, p = 0.26) and dive depths (Day W = 47, p = 0.47; Night W = 45, p = 0.39) between age-classes. Differences in the relationships of mean dive durations with age were evident between age classes (Fig. 4.3). Dive durations increased with age in subadult males, but did not show such an increase within adult males. Rather, a negative relationship was evident for adult males, which indicated that dive durations became shorter with age. Mean dive depths increased with age in subadults and adults (Fig. 4.4). The trend for adult males was influenced by the very deep dives recorded for the oldest male in our sample (Table 4.2). A log-transformation of the dive depth data did not result in a different trend.

Table 4.1: Summary of dive statistics obtained for male southern elephant seals.

	Adults				**Subadults**	
	PM		**PB**			
	Day	**Night**	**Day**	**Night**	**Day**	**Night**
Dives (n)	3 140	5 570	4 326	2 189	18 128	25 570
Surf.Dur (min)	3.1 ± 1.2	3 ± 1.2	2.7 ± 0.5	2.7 ± 0.8	2.3 ± 0.9	2.2 ± 0.8
Dive.Dur (min)	37.6 ± 12.3	31.3 ± 11.1	28.4 ± 6.5	23.4 ± 6.3	32.6 ± 13.8	25.8 ± 11.4
Dive.Dep (m)	779 ± 407	590 ± 448	463 ± 152	366 ± 135	627 ± 223	473 ± 221

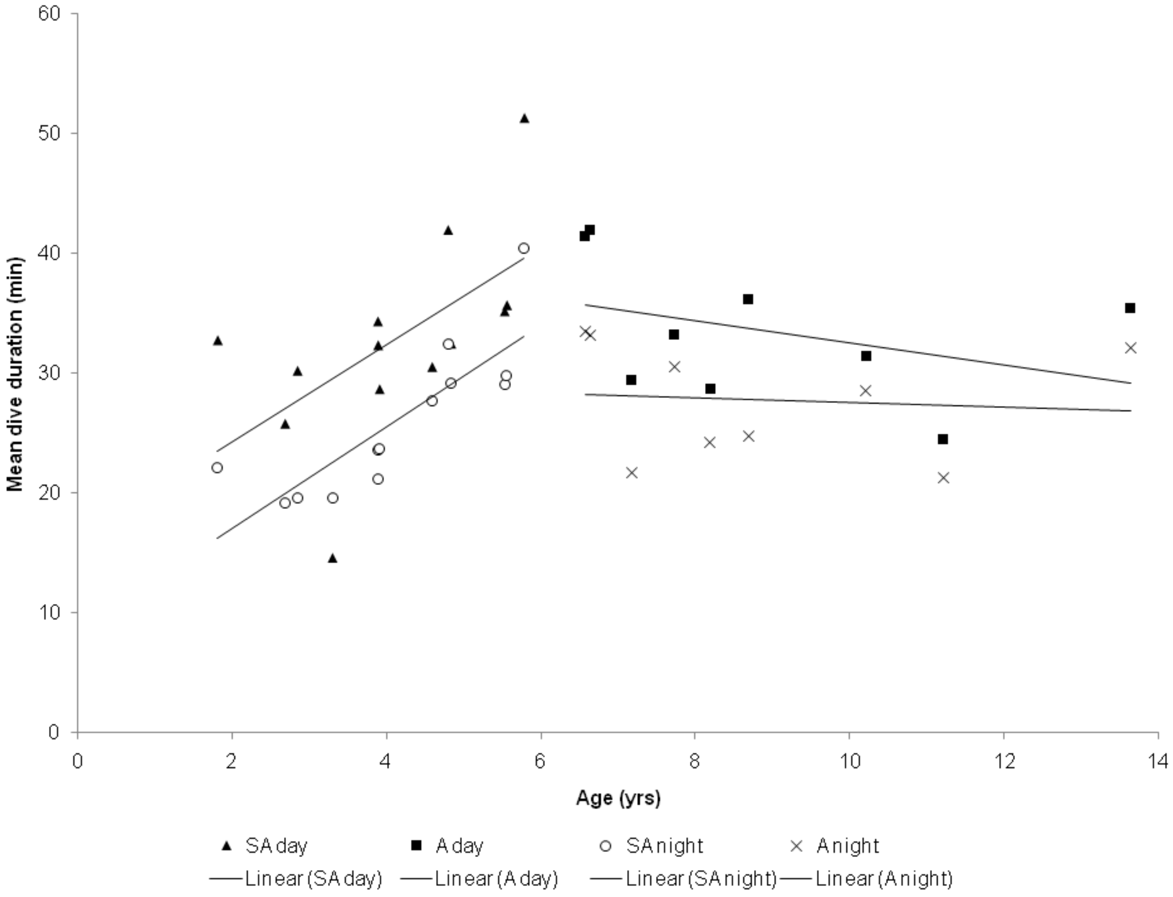

Figure 4.3: Plots displaying the relationship between mean dive duration and the ages of animals in our sample. Separate linear regressions were fitted to subadult daytime (SA day: y = 4.1x + 16.2; R^2 = 0.34), subadult night-time (SA night: y = 4.2x + 8.6; R^2 = 0.7); adult daytime (A day: y = -0.9x + 41.9; R^2 = 0.15) and adult night-time (A night: y = -0.18x + 29.4; R^2 = 0.01) classes.

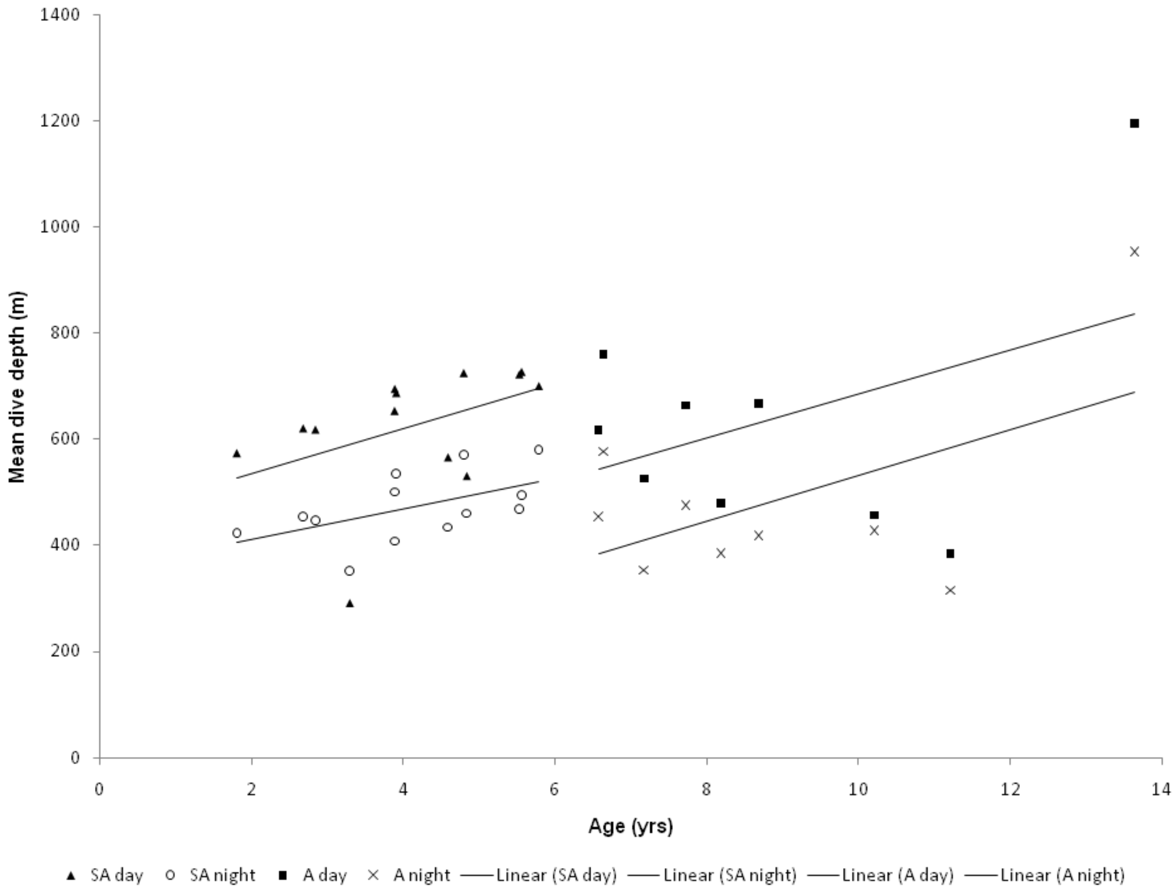

Figure 4.4: Plots displaying the relationship between mean dive depth and the ages of animals in our sample. Separate linear regressions were fitted to subadult daytime (SA day: $y = 42.1x + 451.8$; $R^2 = 0.18$), subadult night-time (SA night: $y = 28.5x + 354.6$; $R^2 = 0.3$); adult daytime (A day: $y = 41.4x + 271$; $R^2 = 0.17$) and adult night-time (A night: $y = 43.1x + 101.3$; $R^2 = 0.29$) classes.

Animals in our sample dived to mean depths of 618.1 ± 258.6 m during daytime dives, and to mean depths of 480.3 ± 272 m at night. Dives lasted for mean periods of 32.5 ± 12.9 min during the day and 26.5 ± 11.2 min at night. These dives were mostly pelagic over deep water (deeper than 2 000 m), though some dives evidently reached the seafloor at depths up to approximately 2 000 m (Fig. 4.5).

Table 4.2: Summary dive data for animals in this study. Deployment = date of deployment; STDL = standard length (in ventral recumbency); Migration = migration stage (PM = post-moult, PB = post-breeding).

Track	Deployment	Age	STDL	Migration	Days (n)	Dives (n)	Surface duration (min)		Dive duration (min)		Dive depth (m)	
							Day	Night	Day	Night	Day	Night
TO340	2004/04/18	1.8	NA	PM	222	4540	2.4 ± 0.8	2.4 ± 0.8	32.8 ± 9.2	22.1 ± 7.5	574.5 ± 152.6	424 ± 135.5
BB253	2005/04/21	2.7	214	PM	106	2616	2.1 ± 0.4	1.9 ± 0.7	25.8 ± 6	19.1 ± 6.1	621.3 ± 123.6	455.1 ± 189.3
OO405	2004/04/18	2.8	NA	PM	229	5236	2.1 ± 0.5	2.0 ± 0.5	30.2 ± 8.3	19.6 ± 4.6	619.0 ± 201.8	448 ± 145.6
RR009	2007/12/21	3.3	210	PM	61	1048	1.6 ± 1	1.6 ± 0.8	14.6 ± 14.6	19.6 ± 22.8	291.9 ± 158.4	351.8 ± 210.9
YY361	2007/05/03	3.9	NA	PM	188	3703	2.1 ± 0.4	1.9 ± 0.6	34.4 ± 8.4	21.1 ± 7.7	654.2 ± 178.8	408 ± 155
OO086	2005/04/19	3.9	260	PM	258	3336	2.1 ± 0.8	2.1 ± 0.9	32.4 ± 11.9	23.6 ± 10.4	695.5 ± 226.7	500.6 ± 218.2
BB263	2006/06/23	3.9	231	PM	143	4054	2.3 ± 0.6	2.1 ± 0.6	28.7 ± 6.5	23.7 ± 10.3	688.1 ± 181.8	535.3 ± 216.3
YY150	2007/12/21	4.6	265	PM	300	8343	2.6 ± 1.4	2.6 ± 1.1	30.5 ± 15.5	27.7 ± 12.1	566.5 ± 234.5	434.3 ± 210.9
OO052_1	2006/04/18	4.8	280	PM	182	3079	2.2 ± 0.7	2.2 ± 0.6	42.0 ± 11.7	32.4 ± 10.5	725.4 ± 214.8	571.8 ± 295.1
BB116	2007/04/21	4.8	NA	PM	115	1808	1.8 ± 0.5	2.1 ± 0.6	32.5 ± 9.5	29.2 ± 7.2	531.4 ± 181.5	460.9 ± 253
BB128	2008/01/05	5.5	293	PM	212	3749	2.7 ± 0.7	2.5 ± 0.8	35.2 ± 13.6	29.0 ± 11.6	722.7 ± 166.6	468.8 ± 203
BB081	2008/01/12	5.6	252	PM	195	3135	2.4 ± 0.7	2.3 ± 0.7	35.7 ± 14	29.8 ± 10.9	727.5 ± 192.3	494.9 ± 233
OO052_2	2007/04/24	5.8	306	PM	199	2736	2.7 ± 0.9	2.8 ± 1.1	51.4 ± 16.5	40.5 ± 14.2	700.7 ± 281.6	580.2 ± 349.3
						Subadults	**2.3 ± 0.9**	**2.2 ± 0.8**	**32.6 ± 14.1**	**26.2 ± 11.7**	**632.4 ± 228.3**	**478.1 ± 228.1**
OO052_3	2008/01/10	6.6	311	PM	211	3264	2.4 ± 0.6	2.4 ± 0.9	41.4 ± 16	33.5 ± 14.6	618.0 ± 243.2	454.2 ± 315.1
WW301	2007/03/25	6.6	NA	PM	142	649	3.3 ± 0.9	3.2 ± 1	42.0 ± 13.1	33.2 ± 11.6	760.3 ± 174.4	576.9 ± 223.1
WW005_1	2007/11/12	7.2	308	PB	61	2052	2.5 ± 0.4	2.4 ± 0.6	29.4 ± 6.7	21.7 ± 5.7	526 ± 177.9	353.9 ± 123.7
GG178	2007/04/22	7.7	NA	PM	118	2086	2.9 ± 0.6	2.8 ± 0.7	33.2 ± 6.5	30.6 ± 6.4	663.6 ± 132.8	476.6 ± 178.2
WW005_2	2008/11/02	8.2	NA	PB	79	1874	2.7 ± 0.6	2.7 ± 1	28.7 ± 6	24.2 ± 6	479.8 ± 155.9	385.8 ± 137.2
PO225_1	2007/03/27	8.7	NA	PM	169	1144	3.4 ± 0.9	3.0 ± 1	36.1 ± 7.4	24.7 ± 8.8	667 ± 137.4	419.7 ± 173
PO225_2	2008/11/09	10.2	NA	PB	77	1365	2.9 ± 0.4	3.0 ± 0.6	31.5 ± 6.3	28.5 ± 7.2	457.1 ± 117.8	428.7 ± 150.8

WR029	2008/11/15	11.2	417	PB	86	1796	2.9 ± 0.4	2.9 ± 0.8	24.5 ± 5	21.3 ± 4.5	384.3 ± 96.5	315.7 ± 111.4
WB057	2008/04/02	13.6	NA	PM	118	2312	4.2 ± 1.4	4.0 ± 1.4	35.4 ± 8.4	32.2 ± 8.3	1196 ± 582.1	953.5 ± 652.9
						Adults	**2.9 ± 0.9**	**2.9 ± 1.1**	**32.3 ± 10.4**	**29.1 ± 10.6**	**595.6 ± 327.7**	**526.8 ± 398.9**

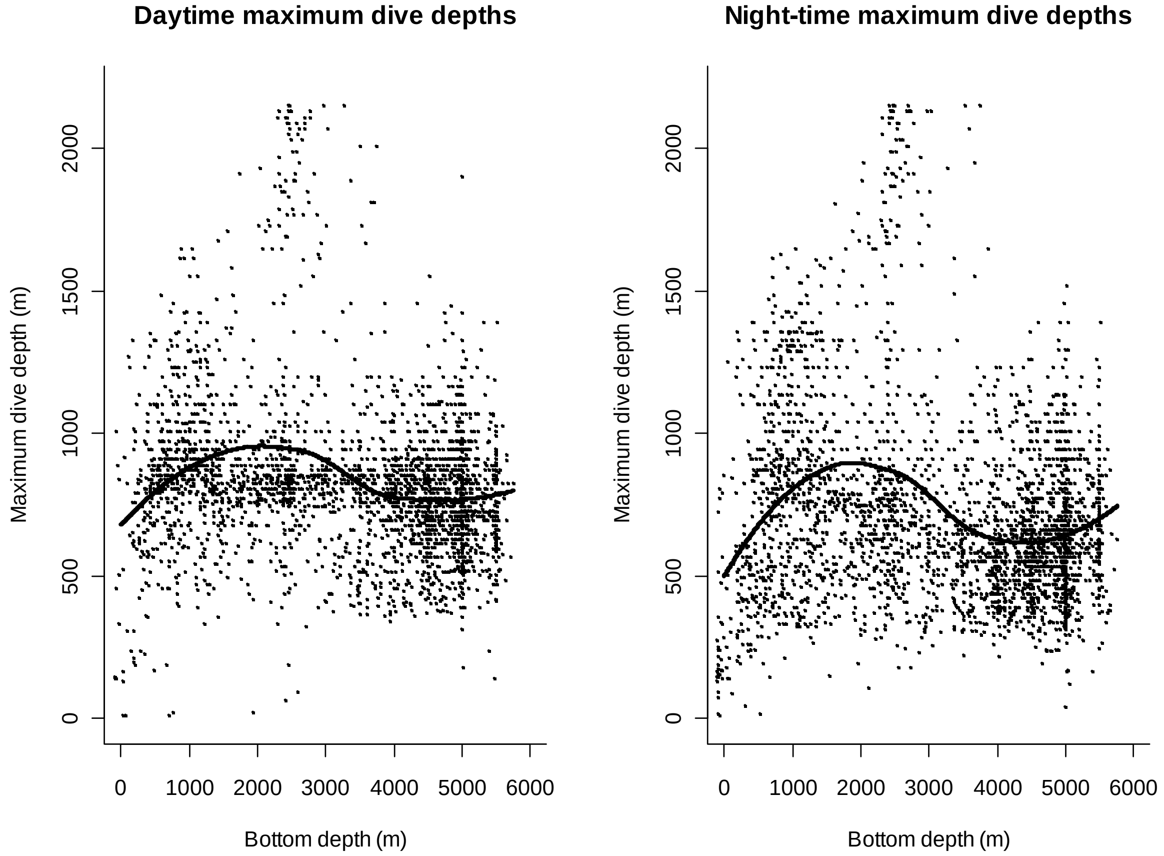

Figure 4.5: Scatter plots illustrating the relationships between day- and night-time dive depths and estimated bottom depths (GEBCO – IOC et al. 2003) for dive recorded in this study. Polynomial regressions were fitted to each plot.

Dive types

U- and W-shaped dives were the most commonly identified dive types for subadult and adult males (Fig. 4.6 and Fig. 4.7). U-shaped dives accounted for 66.4% of all dives recorded for both adult and subadult males, while W-shaped dives were identified in 26.9% of all dives recorded. The remaining dive types accounted for a total of 6.7% of all the dives recorded (DR = 1.8%; R = 1%; SQ = 1.1%; V = 2.8%). Adult males displayed more V-shaped dives overall (4.1%) than subadult males (2.4%). Subadult males displayed more U-shaped dives during daytime dives, than night-time dives, while they undertook more W-shaped dives at night, when compared to daytimes. Adult males displayed the reverse tendency, undertaking more W-shaped dives during daytime, compared to night-time and fewer daytime U-shaped dives than night-time U-shaped dives.

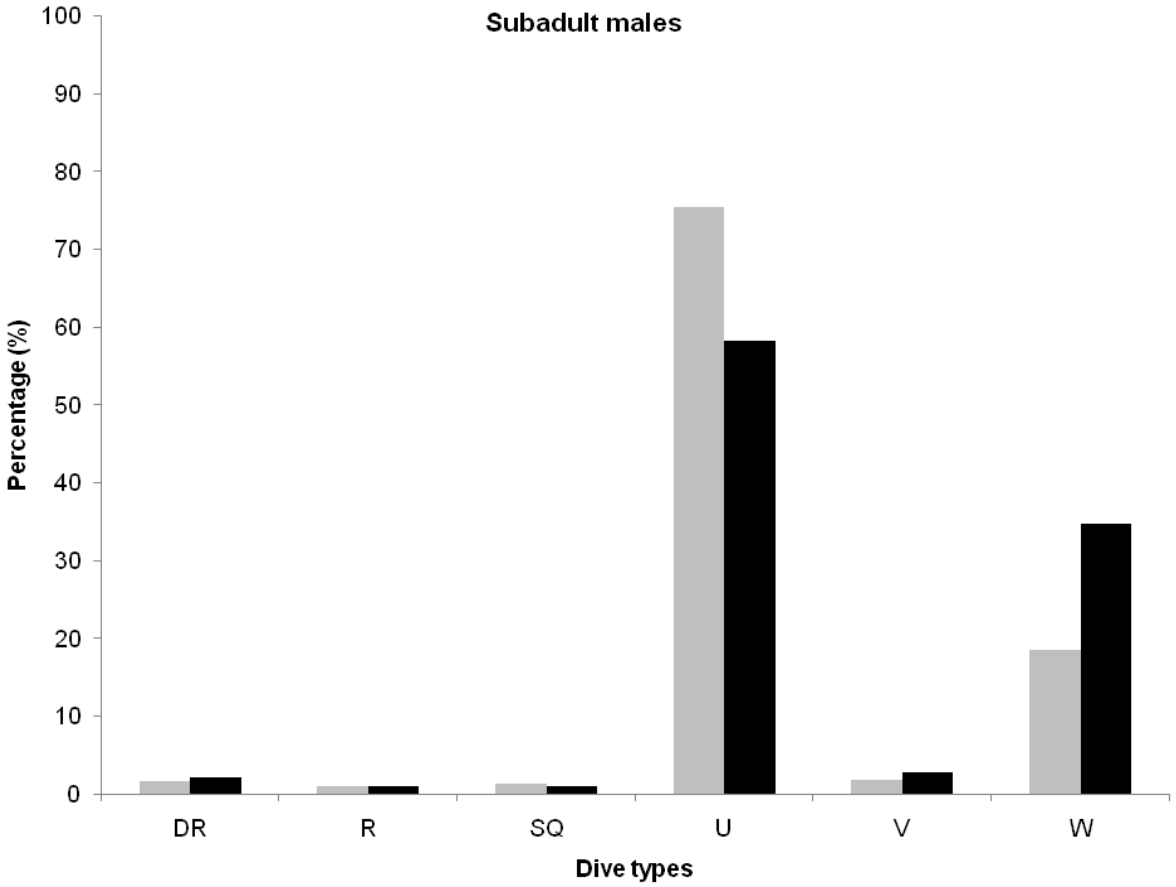

Figure 4.6: Frequency of occurrence histogram of the various dive types identified for subadult males (DR = drift dives; R = root dives; SQ = square dives; U = U-shaped dives; V = V-shaped dives; W = wiggle dives). Black shading indicates dives occurring at night and grey shading indicates daytime dives.

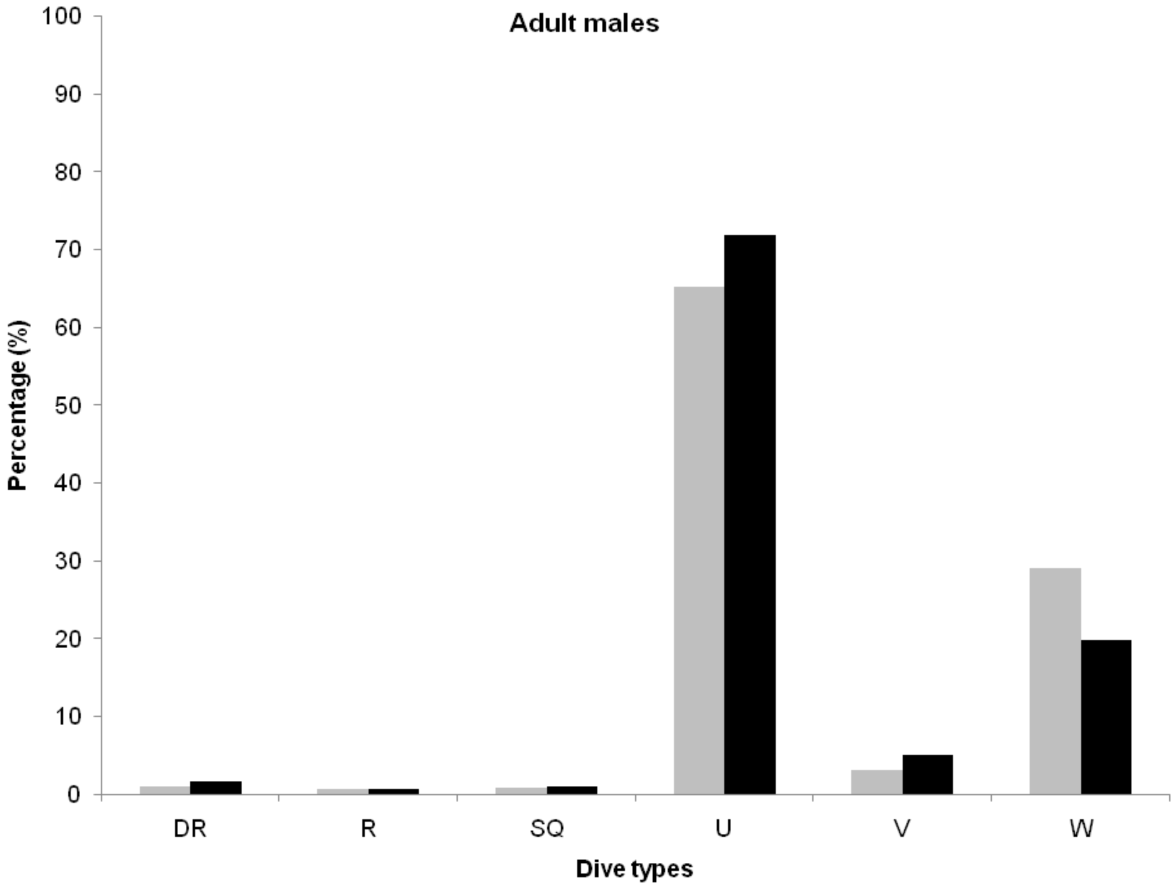

Figure 4.7: Frequency of occurrence histogram of the various dive types identified for adult males (DR = drift dives; R = root dives; SQ = square dives; U = U-shaped dives; V = V-shaped dives; W = wiggle dives). Black shading indicates dives occurring at night and grey shading indicates daytime dives.

Differences in seafloor depth between dive types were statistically significant ($F_{5,53427}$ = 541, $p < 0.001$). A post-hoc Tukey test indicated that seafloor depths were significantly different between the following dive types: R and DR; SQ and DR; U and DR; W and DR; SQ and R; U and R; V and R; U and SQ; V and SQ; W and SQ; V and U. Differences in seafloor depths were not statistically significant between V and DR; W and R; and V and U dives. Summary data indicated such differences to be comparatively small, with only SQ dives undertaken in clearly shallower waters (range of means, excluding SQ dives = 2 733 – 4 069 m; SQ dives = 2 192 – 2 196 m) (Table 4.3).

Table 4.3: Mean (± SD) estimates of seafloor depths for locations where animals exhibited various dive types.

Dive type	Adults Dives (n)	Seafloor depth (m)	Subadults Dives (n)	Seafloor depth (m)
DR	215	3 484 ± 1 386	816	3 254 ± 1 853
R	108	3 383 ± 1 267	515	4 069 ± 1 344
SQ	146	2 196 ± 1 784	527	2 192 ± 1 960
U	11 370	2 733 ± 1 448	27 383	3 245 ± 1 743
V	674	2 790 ± 933	1 088	3 627 ± 1 575
W	4 029	3 528 ± 1 175	12 514	3 955 ± 1 457

Forage effort dives

Adult forage effort dives were distributed amongst a few areas within the minimum convex polygons of adult male activity (Fig. 4.8 and Fig. 4.9). Daytime forage effort was higher in a concentrated area to the north of Marion Island, within a distance of ~ 360 km. Also, higher forage effort dives were recorded in an area north-west of the island, particularly between the Prince Edward fracture zone (PEFZ), the Andrew Bain fracture zone (ABFZ) and the SWIR. Other areas of increased daytime forage effort include an area ~ 1 200 km to the north-west of the island and north of the SAF, as well as various scattered localities in close proximity to the SWIR. Night-time forage effort dives were also concentrated in the area bordered by the ABFZ, the PEFZ and the SWIR. Further, an area of increased forage effort dives was identified approximately 850 km west of Marion Island, immediately north of the SWIR. No clear relationship existed between bottom time residuals of U-shaped dives and estimates of the water depths (Daytime dives: cor = -0.02, p = 0.29; Night-time dives: cor = -0.02, p = 0.25).

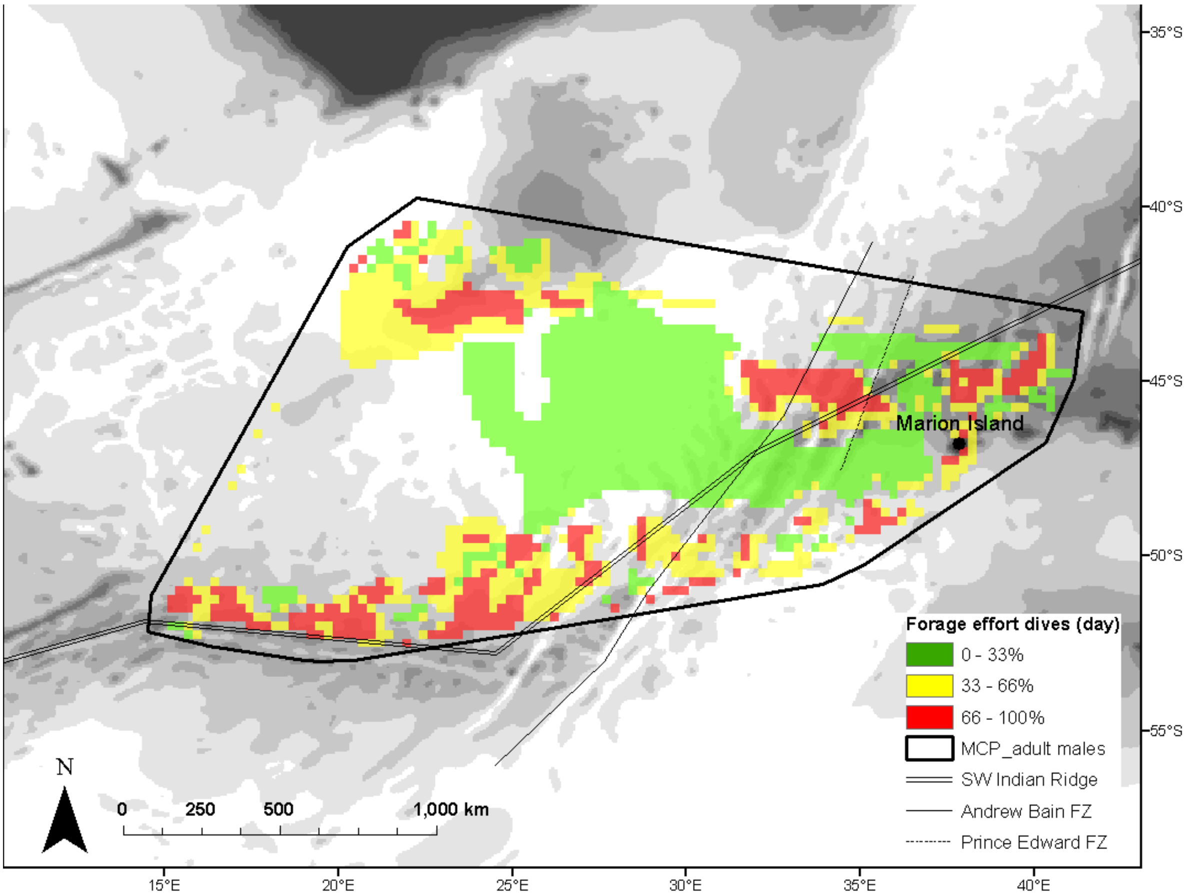

Figure 4.8: Map indicating daytime ratios of forage effort per day (ratio of U-shaped dives, with greater-than-expected bottom times) for the area utilised (minimum convex polygon – MCP) by adult male southern elephant seals. Bathymetric features highlighted on the map include the Southwest Indian Ridge (SW Indian Ridge), Andrew Bain Fracture Zone (Andrew Bain FZ) and Prince Edward Fracture Zone (Prince Edward FZ).

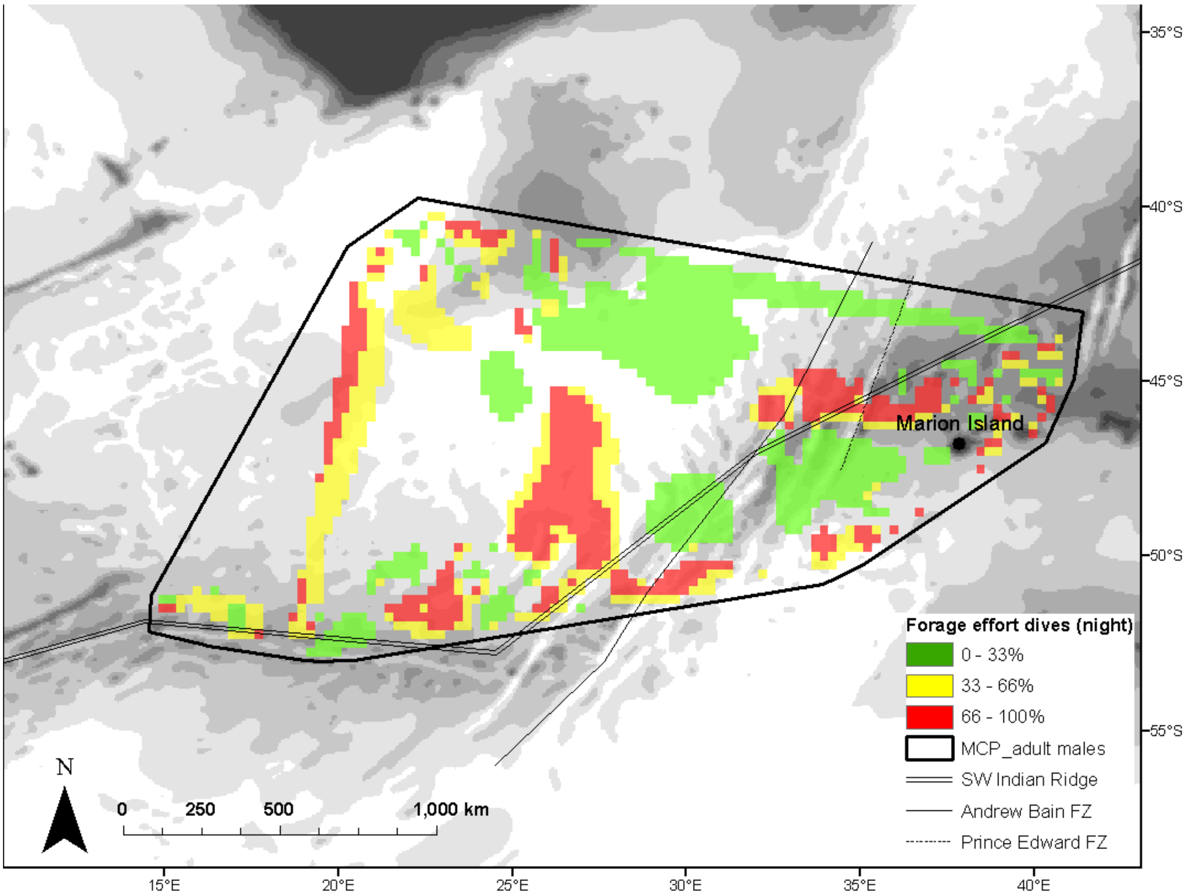

Figure 4.9: Map indicating night-time ratios of forage effort per day (ratio of U-shaped dives, with greater-than-expected bottom times) for the area utilised by adult male southern elephant seals. Bathymetric features are the same as for Fig. 4.8.

Daytime subadult male forage effort dives were concentrated in an area extending from ~ 15°E – 35°E and from ~ 42°S – 56°S (Fig. 4.10). A few other areas of increased forage effort were identified further distant from Marion Island and are shown in Fig. 4.10. Night-time forage effort dives undertaken by subadult males were less concentrated in the areas described for daytime forage effort dives. Specific areas of increased forage effort dives were identified in an area extending from ~ 4°E – 16°E and ~ 46°S to 65°S (Fig. 4.11). Another area of increased night-time forage effort was identified ~ 700 km south of Marion Island. Bottom time residuals of daytime dives undertaken by subadult males showed a weak, but significant relationship with estimates of water depth (cor = 0.04, p < 0.001). No such relationship was evident for dives undertaken at night (cor = -0.01, p = 0.2).

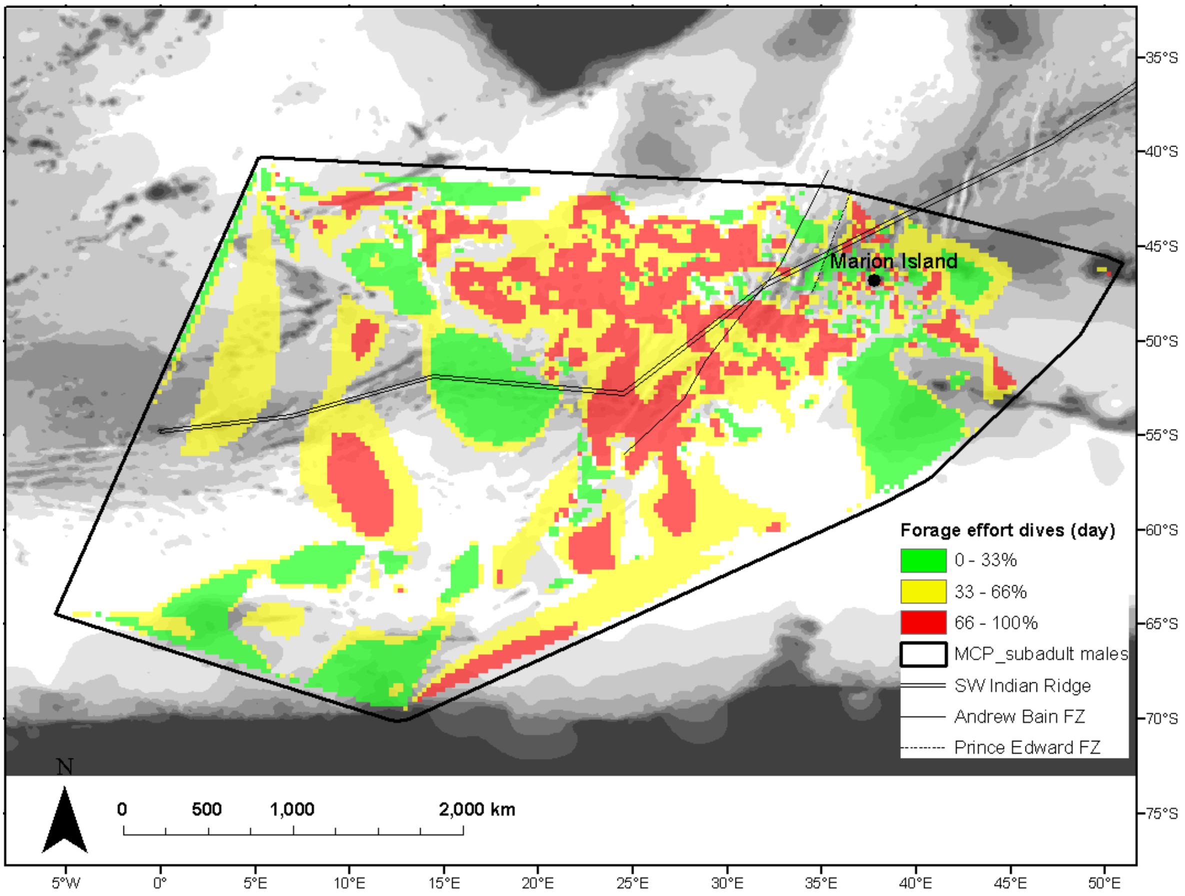

Figure 4.10: Map indicating daytime ratios of forage effort per day (ratio of U-shaped dives, with greater-than-expected bottom times) for the area utilised by subadult male southern elephant seals. Bathymetric features are the same as for Fig. 4.8.

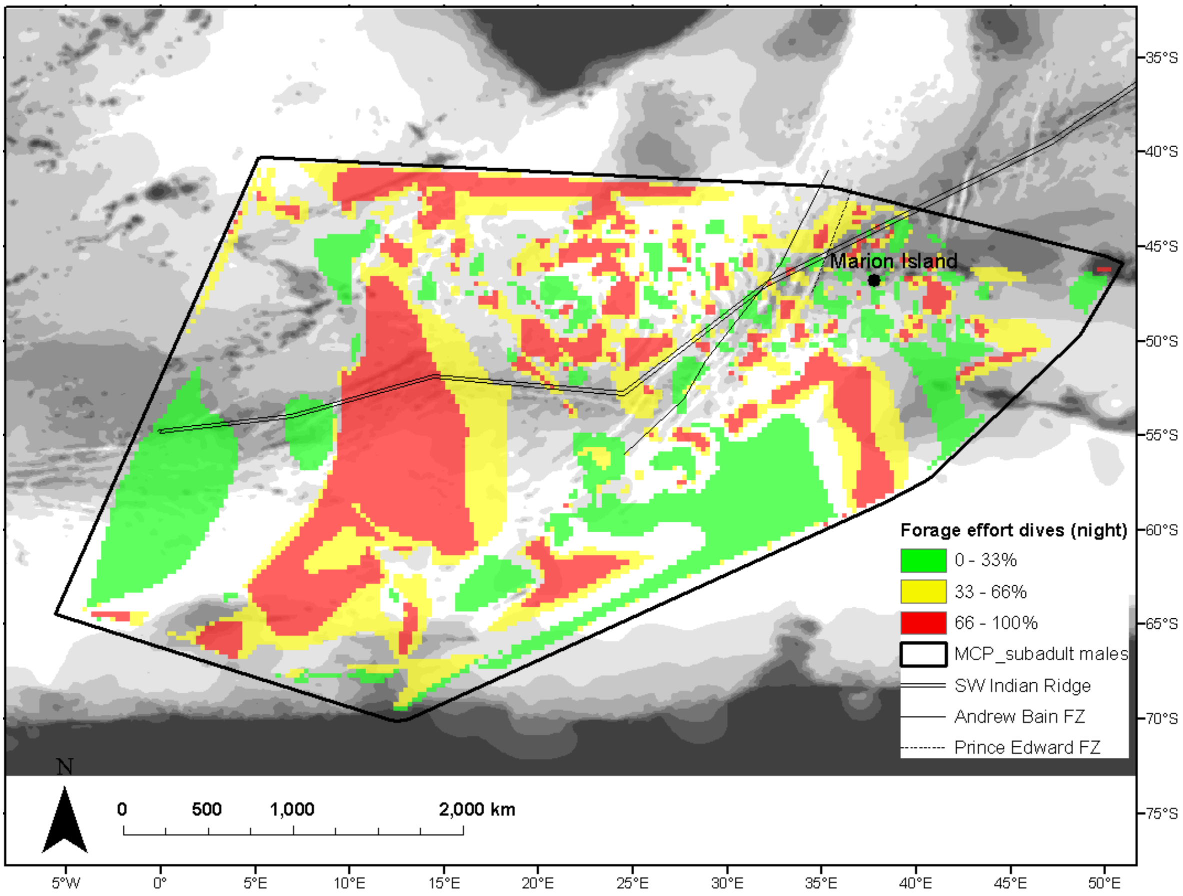

Figure 4.11: Map indicating night-time ratios of forage effort per day (ratio of U-shaped dives, with greater-than-expected bottom times) for the area utilised by subadult male southern elephant seals. Bathymetric features are the same as for Fig. 4.8.

Diel vertical strategy

Adult and subadult males mostly displayed positive diel vertical migration (DVM) throughout their migrations (e.g. Fig. 4.12a). Some adult animals displayed much variation in DVS throughout their migrations (and also between migrations by the same individuals), often exhibiting negative DVS (Fig. 4.12b-d). Time-series scatterplots for all males tracked are reported in Appendix B.

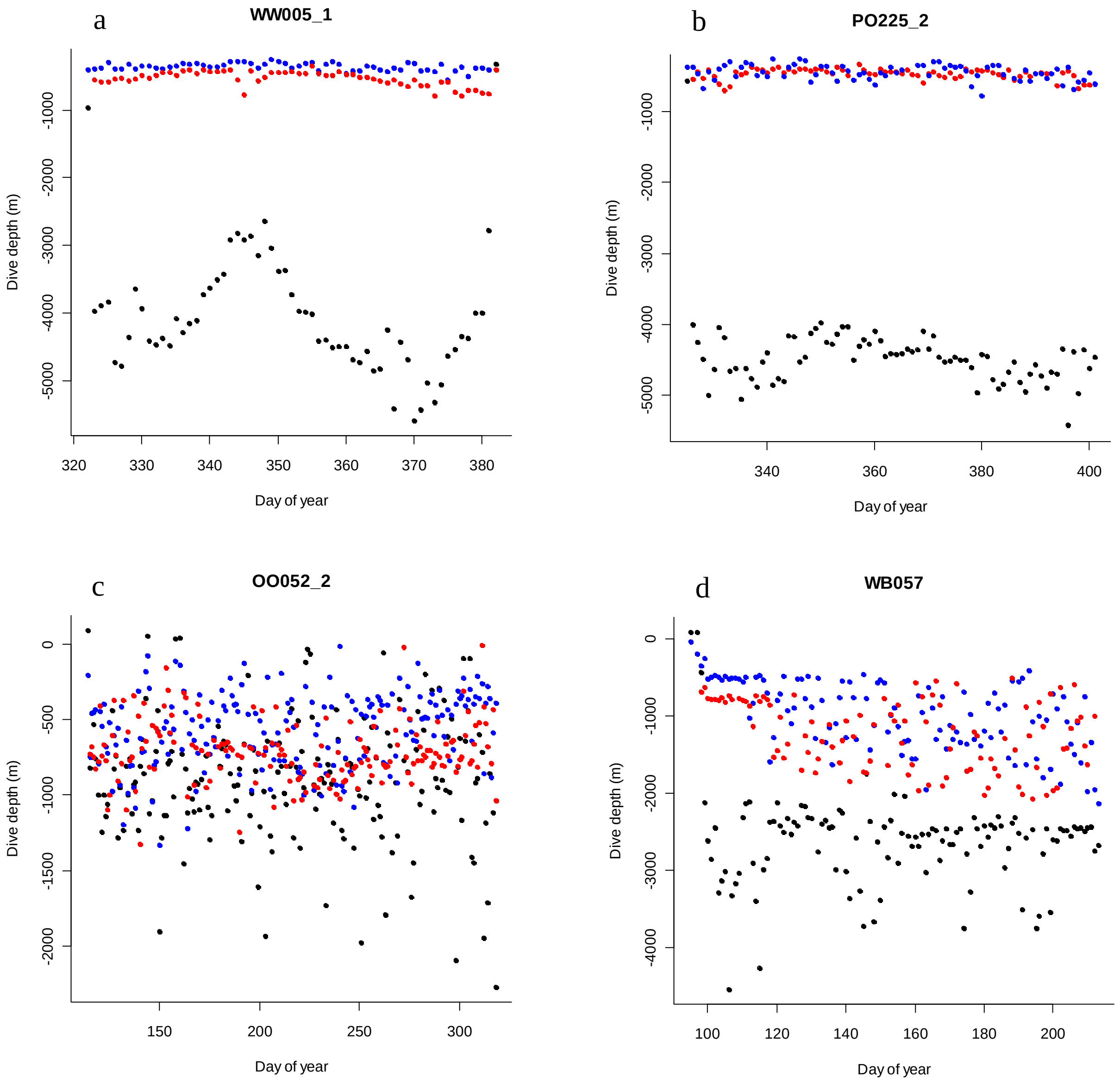

Figure 4.12: Scatterplots indicating the daily mean dive depths recorded for selected adult males during the day and at night in relation to estimates of bottom depth. Red dots = mean daytime dive depths (m); blue dots = mean night-time dive depths (m); black dots = estimates of bottom depth (m) for daily averaged location obtained through the Gebco atlas (IOC et al. 2003).

Subadult males displayed vertical diel variation, diving deeper during daytimes than at night when foraging over deeper waters (Fig. 13a), as well as when foraging in shallower water (Fig. 13b).

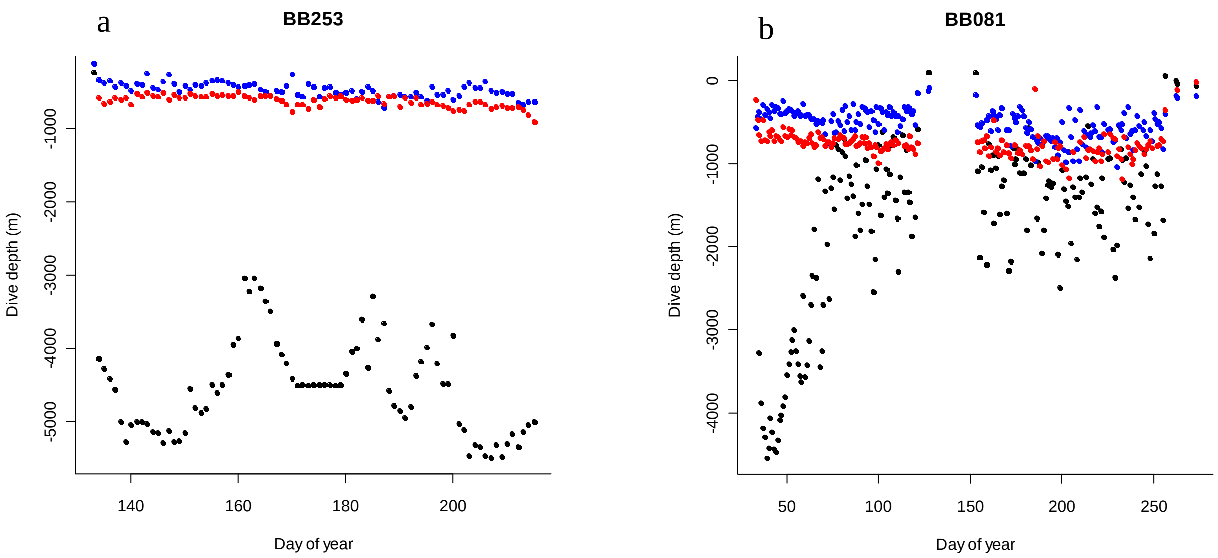

Figure 4.13: Scatterplots indicating the daily mean dive depths recorded for selected subadult males during the day and at night in relation to estimates of bottom depth. Red dots = mean daytime dive depths (m); blue dots = mean night-time dive depths (m); black dots = estimates of bottom depth (m) for daily averaged location obtained through the Gebco atlas (IOC et al. 2003).

Discussion

This study describes the water column use of male southern elephant seals from Marion Island. The predominant south-western movement of animals away from the island is a similar trend in overall movement to that shown for female seals from this population (chapter 3). Adult males tended not to travel as far as subadults and stayed in closer proximity to the island.

Dive depths and durations

Male southern elephant seals from Patagonia (Peninsula Valdés) predominantly display two dive strategies, either diving benthically to depths of less than 200 m in shallow waters on the South American continental shelf, or diving pelagically in deeper waters to depths averaging approximately 400 m off the continental shelf (Campagna et al. 1999). Dives on the shelf last for mean periods of 15.1 min, while dives off the shelf are longer (mean duration of

23.1 min). Similar strategies were reported for animals from Macquarie Island (Hindell et al. 1991), where males reportedly dive to mean depths of 398 ± 164 m and for durations of 24 ± 9 min. Biuw et al. (2010) reported that male southern elephant seals tracked from Bouvetøya tend to target the Dronning Maud Land shelf (Antarctica), where they evidently largely undertake benthic foraging dives to depths of ca. 400-500 m.

The dive depths and durations recorded in this study indicate that male southern elephant seals from Marion Island tend to dive to deeper depths and for longer periods of time than male elephant seals from other populations. Marion Island is surrounded by deep water, though a few prominent shelf areas with shallower water masses, such as the Del Caño Rise and the Conrad rise are in relative close proximity (less than 700 km from Marion Island). Male southern elephant seals from Marion Island did not travel to such shelf areas, but rather remained in deep water. In such water masses dives commonly did not reach the seafloor and animals evidently pursued pelagic prey.

Mean dive depths and durations did not differ substantially between adult- and subadult males. However, the relationships between dive duration and age showed different trends between age classes. Subadult males appeared to rapidly increase mean dive durations between the ages of two and six, while adult animals did not exhibit this positive relationship, but rather a negative one where the older animals tended to dive for shorter periods of time. Dive durations have previously been shown to be influenced by physiological capacity associated with body size (Hindell et al. 2000; Irvine et al. 2000; see chapter 5). The trends observed here for the relationship between dive duration and age is therefore likely a direct result of increased physiological capacity associated with increases in size during the first six years of life. A similar positive trend was exhibited in dive depths for subadult animals. The trend for adult animals was strongly influenced by the extreme diving of the oldest animal tracked in our sample, which often dived to depths deeper than 2 000m (chapter 2). The remaining animals did not exhibit an increase in dive depths associated with age. These trends are likely to be further influenced by the migration stage of a particular animal. Seals participating in the breeding haulout and defending harems are affected by the costs associated with increased energy expenditure (Galimberti et al. 2007), and are therefore less likely to dive to deeper depths and longer periods of time. We did not take the influence of migration stage into account for this investigation due to insufficient sample sizes, but we consider differences in condition between migration stages to likely further influence dive depths and durations.

Dive types

U-shaped dives were the dominant dive type identified in our study, followed by W-dives. The dominance of U- and W-dives compares well with results obtained for female animals from the same population (chapter 3). SQ-dives are mostly associated with benthic diving, whereby the animals reaching the seafloor results in the 'flat' depth line in a time-depth profile. Since the animals in our samples rarely dived to the seafloor, the rarity of SQ dives in our sample was not surprising. SQ dives were, however, mostly carried out in areas of evidently shallower bathymetry than other dives types. The estimated seafloor depths for such areas (adults: 2 196 ± 1 784 m; subadults: 2 192 ± 1 960 m) are generally still deeper than the maximum dive depths recorded for animals in our study (with the exception of WB057 that dived to a maximum depth of 2 149 m). The prevalence of SQ dives in areas of comparatively shallower bathymetry may also be indicative of errors in the seafloor depth estimates and be suggestive of true seafloor depths (Padman et al. 2010). DR dives were also rare in our sample and likely the result of comparatively recent changes to the onboard abstraction algorithm employed on the SRDLs, resulting in slight difference to the recording of inflection points (Biuw pers. comm.).

Subadult animals undertook more U-shaped dives during the day, when compared to night-time dives. The number of W-dives undertaken by these animals showed the reverse pattern, with animals undertaking more W-dives at night, compared to daytime. This is likely a by-product of diel variation in dive depths, whereby shallower night-time dives are resulting in animals being physiologically capable of spending longer times at preferred depths, and also making adjustments to their dive depths. Adult males showed a different pattern compared to subadults and undertook more W-dives during the day, when compared to night-time dives. Also, U-shaped dives were more numerous at night than during the day in adults. This may indicate more directed foraging movements (and more concentrated foraging efforts) at night in adult males, whereby animals are spending less time searching for optimal foraging depths and are able to travel directly to these profitable depths. However, the difference in trend between males and subadults is difficult to explain. Subadults display a strategy more similar to those of female seals from the same population (chapter 3), and this is possibly by-product of shallower dive depths at night allowing the animals more time to adjust their foraging depths at various points - thereby generating more W-shapes to the time-depth profiles at night.

Areas of forage effort

The maps generated in this assessment indicate that areas of increased forage effort were dispersed throughout the areas visited by male southern elephant seals from Marion Island. Adult males displayed consistently increased levels of forage effort between day- and night-times in a few areas, notably in an area bordered by the SWIR, ABFZ and PEFZ. The intersection of the ABFZ with the SWIR has previously been highlighted as a potentially important area for elephant seals from Marion Island (Tosh 2010), and it is likely that increased water turbulence associated with these structures are leading to increases in productivity in the vicinity.

Remaining areas of increased forage effort often differed between day-and night-times and much variability was evident. Subadult males appeared to concentrate their daytime forage effort dives in a large area either side of the SWIR, but within a distance of approximately 1 700 km west of Marion Island. Night-time forage effort dives were less concentrated in this area and appeared more concentrated in areas extending further away from the island. Notably, areas of increased forage effort did not appear to be associated with specific areas of shallower bathymetry and there was evidently no relationship between the relative proportions of time spent at the bottoms of forage-type (U-shaped) dives and the estimated water depths of dive locations. This is in contrast to the behaviour of males from other populations that are known to target shelf and other areas of shallow bathymetry, where they often undertake benthic dives (Hindell et al. 1991; Campagna et al. 1999; Biuw et al. 2010).

This investigation did not take into account the potential influences of differences in productivity associated with mesoscale oceanographic features, such as eddies or meanders. It is reasonable to assume that increases in ocean productivity associated with such features are likely to influence the locations of increased forage effort displayed by male elephant seals, and future investigations should aim to take this into account. Our sample further did not allow for inter-annual comparisons of areas where elephant seals displayed increased forage effort dives.

Forage strategy

Adult males in our sample broadly adopted strategies that resulted in positive diel variation in dive depths, while strategies that resulted in neutral and negative diel variation tended to be less common. Subadult males displayed much variation in diel strategy throughout the area utilised. Areas where both adults and subadults displayed negative diel variation was relatively common, and this strategy was evidently more often exhibited by males, when compared to female elephant seals from Marion Island (chapter 3). Despite this, only one animal (RR009) dived to deeper mean depths during the night, compared to daytime dives (Table 4.2). This suggests that individuals varied their diel dive strategies substantially throughout their migrations. Indeed, closer investigations into individual time-series maps of dive depths between day- and night (Fig. 4.12) suggest that animals often switch between strategies. This plasticity in strategy suggests that male elephant seals are likely less dependent on vertically migrating prey than females, but are able to successfully switch to prey at deeper depths that do not exhibit substantial vertical migration. This provides some support for active forage segregation between sexes in this species (see chapter 5).

We did not take into the account the potential influences of spatial and temporal variation in light intensity associated with cloud cover. While heavy cloud cover may have influenced the prevalence of neutral diel strategies in our sample, due to less substantial vertical migrations undertaken by prey, it does not explain the prevalence of animals displaying negative diel variation strategies.

Conclusion

Dive data recorded for male southern elephant seals from Marion Island indicated substantial variation in forage strategy, with animals often switching between strategies that resulted in positive diel variation and neutral or even negative diel variation. Animals in our sample did not specifically target areas of shallower bathymetry and relatively few dives to the seafloor were identified. Adult males tended to focus their forage efforts in closer proximity to Marion Island than subadult males, though much variation in areas of increased forage effort was evident throughout the areas utilised by both age-classes.

CHAPTER FIVE: SEGREGATION IN A SEXUALLY DIMORPHIC MAMMAL: A MIXED-EFFECTS MODELLING ANALYSIS OF DIVING BEHAVIOUR IN SOUTHERN ELEPHANT SEALS*

Abstract

Sexual segregation in habitat use occurs in a number of animal species, including southern elephant seals, where differences in migration localities and dive behaviour between sexes have been recorded. Due to the extreme sexual size dimorphism exhibited by southern elephant seals, it is unclear whether observed differences in dive behaviour are due to increased physiological capacity of males (when compared to females) or differences in activity budgets and foraging behaviour. Here we use a mixed-effects modelling approach to investigate the effects of sex, size, age and individual variation on a number of dive parameters measured on southern elephant seals from Marion Island. Although individual variation accounted for substantial portions of total model variance for many response variables, differences in maximum- and targeted dive depths were always influenced by sex, and only partly by body length. Conversely, dive durations were always influenced by body length, while sex was not identified as a significant influence. These results support hypotheses that physiological capability associated with body size is a limiting factor on dive durations. However, differences in vertical depth use appears to be the result of differences in forage selection between sexes, rather than a by-product of the size dimorphism displayed by this species. This provides further support for resource partitioning and possible avoidance of inter-sexual competition in southern elephant seals.

* Published as: McIntyre, T, Tosh, C.A., Bornemann, H., Plötz, J. & Bester, M.N. 2010. Segregation in a sexually dimorphic mammal: a mixed-effects modelling analysis of diving behaviour in southern elephant seals. *Marine Ecology Progress Series* 412 293-304.

Introduction

Sexual segregation has been defined as the separation of members of a species, such that sexes live apart, either singly or as single-sex groups (Wearmouth & Sims 2008). It is a phenomenon present in reptiles (Ford & Hampton 2009), fish (Mucientes et al. 2009), birds (Gonzales-Solis et al. 2008; Morales et al. 2008; Palacin et al. 2009) and mammals. In mammals, sexual segregation has been studied mostly in terrestrial species, particularly ungulates and other group-living mammals where it appears to be very common (MacFarlane & Coulson 2007; Ciuti & Apollonio 2008; Hay et al. 2008; Li & Jiang 2008; Shannon et al. 2008). It is less well documented in marine mammals, though it appears to play an important role for various cetacean species, notably for species that live in social groups (Whitehead & Weilgart 2000; Martin & da Silva 2004). Recent advances in satellite-tracking devices for marine species have led to new understandings of the pelagic phases of pinniped lifecycles across the globe. As a result, sexual segregation in migration patterns and depths utilised has increasingly been reported for a number of seal species (Page et al. 2005; Wolf et al. 2005; Breed et al. 2006; Staniland & Robinson 2008).

Mechanisms presented to explain such difference in behaviour between sexes include (1) predator avoidance, (2) forage selection, (3) differences in activity budgets, (4) thermal niche-fecundity in ectotherms, and (5) social factors (Ruckstuhl 2007; Staniland & Robinson 2008; Wearmouth & Sims 2008). Notably, many of these hypotheses are associated with sexual size dimorphism and predict positive correlations of sexual segregation with sexual size dimorphism.

Southern elephant seals are extremely sexually dimorphic, with males sometimes being up to ten times larger than females (Le Boeuf & Laws 1994b). Adult breeding animals haul out at breeding colony sites twice during a year – once during the breeding period (austral spring), and once for the annual moult (austral mid to late summer). Segregation in forage locations between the sexes in southern elephant seals have been reported for animals from various localities (Campagna et al. 1995; McConnell & Fedak 1996; Campagna et al. 1999; Bornemann et al. 2000; Tosh et al. 2009). Similarly, a number of studies demonstrate segregation in dive behaviour, with females foraging mostly pelagically while males tend to either forage benthically or show greater variation in forage strategy, often employing both pelagic and benthic strategies (Hindell et al. 1991; McConnell et al. 1992; Campagna et al. 1995; Jonker 1997; Malherbe 1998; Campagna et al. 1999; Field et al. 2005b).

Such differences in forage locations and dive behaviour are thought to be associated with sex-specific foraging strategies in this species, with males reportedly adopting more risky foraging strategies in order to maximise early growth (Lewis et al. 2006; Field et al. 2007a). Such segregation has largely been attributed to inter-sexual competition avoidance in this species (Field et al. 2005b; Lewis et al. 2006). While such investigations reported clear differences in foraging strategies between males and females, no attempts were made to quantify the effects of body size differences between sexes. This is important since the extreme sexual dimorphism of this species is likely to influence dive parameters and cloud the potential influence of sex versus body size on the dive behaviour of elephant seals.

Here we investigate sexual differences in dive behaviour of southern elephant seals from Marion Island. Our aims were specifically to determine if differences in dive parameters between sexes were a result of inherent sex-related traits or merely a by-product of size differences between sexes. Because of the unbalanced nature of available data, we utilised a mixed-effects modelling approach to elucidate the effects of sex, standard length and age on the depth utilisation of elephant seals.

Methods

Satellite-tag deployments

A total of 57 satellite-relay data loggers (Sea Mammal Research Unit, University of St Andrews, Scotland) were deployed on southern elephant seals of known age and sex hauled out at Marion Island (46°54’S; 37°45’E). Deployments were made on known individuals, born and flipper-tagged on the island as part of a long-term mark-recapture investigation (Bester 1988b; de Bruyn et al. 2008). Two types of satellite-relay data logger (SRDL) were used in this investigation – 33 SRDL Series 9000 and 24 SRDL-CTD devices. Devices were glued onto the cranial pelage of immobilised animals (for further details see Tosh et al. (2009)). All SRDLs were programmed to measure pressure every 4 s during each dive of the animal. Only dives deeper than 6m were recorded. Detailed dive data were compressed onboard the instruments, prior to transmission, using a broken-stick algorithm to provide four dive points reflecting the greatest inflections, as well as the maximum depth reached within the dive (Fedak et al. 2001; Boehme et al. 2009). This information was relayed via service Argos (Argos 1996), along with environmental data (SRDL Series 9000 devices recorded temperature profiles, while SRDL-CTD devices recorded temperature and conductivity profiles), and position estimates calculated from Doppler shift measurements in successive uplinks. All dive and environmental meta-data are available via the PANGAEA information system (www.pangaea.de).

For the purposes of this investigation we only included data obtained from animals where deployments were made prior to post-moult migrations (as opposed to post-breeding migrations). Also, only tracks obtained from animals with measured standard length data (with the seal in ventral recumbency) and known ages at the time of deployment were included. Few mass measurements were available for the study animals, precluding the inclusion of mass as an indication of body size. We further removed data obtained from the largest males and smallest females of known lengths (males: n = 2; females: n = 3) in order to ensure substantial overlap in standard lengths between sexes and remove a possible confounding effect between sex and standard length (see Results). This resulted in data being retained from 20 (12 females and 9 males; Table 5.1) tracks for this study.

Filtered tracks (see Tosh et al. 2009) were plotted in Arcview 3.3 (ESRI 1998). Space use and the extent of movements were calculated using Animal Movement Analyst (Hoodge & Eichenlaub 1997). Kernel density estimators based on all locations further than 200 km from Marion Island were calculated in order to determine space use probabilities (95% and 50%) for females and males separately. Minimum convex polygons were drawn to determine the maximum extent of movements for both sexes.

Table 5.1: Dive characteristics of selected southern elephant seal tracks used in this investigation. Only dives with a positive residual value resulting from the regression of bottom time as a function of maximum dive depth and dive duration (indicating increased forage effort) were included. Stdl = standard length; DD = dive duration; MD = Maximum depth; ED = Exploited dive depth. Values are presented as means (± SD) of individual seal averaged values.

Animal	Track	Sex	Year	Age (yrs)	Stdl (cm)	DD$_{\text{DAY}}$	DD$_{\text{NIGHT}}$	MD$_{\text{DAY}}$	MD$_{\text{NIGHT}}$	ED$_{\text{DAY}}$	ED$_{\text{NIGHT}}$
BB081	BB081	m	2008	5.3	252	36 ± 12	29 ± 10	732 ± 149	465 ± 219	687 ± 142	439 ± 197
BB128	BB128	m	2008	5.3	293	38 ± 13	26 ± 10	743 ± 148	426 ± 166	723 ± 155	375 ± 147
BB253	BB253	m	2005	2.6	214	24 ± 5	19 ± 4	563 ± 90	457 ± 164	530 ± 90	406 ± 153
BB263	BB263	m	2006	3.7	231	30 ± 5	22 ± 6	684 ± 130	501 ± 175	632 ± 128	445 ± 176
GG335	GG335_2	f	2008	8.3	235	34 ± 12	30 ± 9	556 ± 150	422 ± 120	518 ± 146	388 ± 118
OO021	OO021_2	f	2008	6.3	225	34 ± 8	25 ± 6	546 ± 102	394 ± 92	520 ± 100	355 ± 91
OO052	OO052_1	m	2006	4.6	280	43 ± 13	32 ± 11	722 ± 181	572 ± 261	682 ± 183	526 ± 258
OO086	OO086	m	2005	3.5	260	33 ± 10	23 ± 8	682 ± 194	498 ± 164	615 ± 182	428 ± 155
OO418	OO418	f	2008	6.4	230	28 ± 8	21 ± 6	550 ± 154	367 ± 164	504 ± 145	327 ± 160
PO043	PO043_1	f	2007	8.3	254	18 ± 15	24 ± 23	310 ± 142	332 ± 142	265 ± 142	291 ± 146
RR009	RR009	m	2008	3.2	210	16 ± 14	20 ± 19	310 ± 140	405 ± 203	270 ± 132	360 ± 207
WW058	WW058	f	2008	7.3	244	31 ± 8	24 ± 7	555 ± 178	372 ± 187	510 ± 169	330 ± 178
WW061	WW061	f	2008	7.3	233	33 ± 6	25 ± 5	592 ± 109	407 ± 128	550 ± 106	361 ± 123
YY150	YY150	m	2008	4.2	265	36 ± 14	28 ± 9	638 ± 200	423 ± 179	599 ± 200	373 ± 166
YY189	YY189_1	f	2006	2.5	222	35 ± 6	23 ± 5	625 ± 98	427 ±108	579 ± 97	383 ± 106
	YY189_2a	f	2007	3.3	224	28 ± 9	20 ± 5	563 ± 102	432 ± 98	524 ± 100	390 ± 100
	YY189_3a	f	2008	4.3	242	30 ± 10	24 ± 7	522 ± 116	372 ± 97	491 ± 119	334 ± 96
YY193	YY193_2	f	2008	4.3	224	31 ± 10	24 ± 9	502 ± 115	286 ± 128	467 ± 114	254 ± 125
YY264	YY264_2	f	2008	4.4	236	32 ± 10	23 ± 7	497 ± 133	297 ± 125	467 ± 132	260 ± 123
YY348	YY348_2	f	2008	4.4	227	35 ± 10	22 ± 6	571 ± 173	370 ± 185	537 ± 166	329 ± 176

Dive analyses

We removed all incomplete (containing missing values) or unrealistic (containing sequential time values that are not chronological) dive sequences prior to analysis. Due to the compressed format that dive data are received in, estimating times spent by animals within various depth layers are problematic. We therefore used a simple interpolating algorithm, assuming constant swim speeds and directions between transmitted dive points, to calculate estimated times spent within various depth layers (100 m increments from the surface to 1 000m, thereafter 1 000-1 250 m, 1 250-1 500 m, 1 500-2 000 m, and 2 000 m+) for each transmitted dive profile (see chapter 2 for further details). We then identified the mid-depth value of each depth layer in which an animal spent the most time during any particular dive (e.g. if the seal spent the largest amount of time in the 0 to 100 m depth layer, then 50 m). This was referred to here as the exploited depth.

To account for variation in dive behaviour associated with differing activity (e.g. foraging, travelling or resting) we identified individual dives with longer-than-average bottom times for each track (Bailleul et al. 2008). Accordingly, we calculated bottom time as the time spent by an animal at depths exceeding 80% of the maximum depth point for that dive (Lesage et al. 1999; Schreer et al. 2001; Burns et al. 2008). We then used linear regressions to calculate average bottom times for dives with given dive durations and maximum dive depths (Bailleul et al. 2008). The residual values obtained from these regressions then identified individual dives as being characterised by longer- and shorter than average bottom times. Dives with positive residuals (indicating longer-than-average bottom times) were assumed to suggest increased foraging effort and were retained for further analysis.

Diel variation in dive behaviour has been documented for a number of seal species, including southern elephant seals (Jonker & Bester 1994; Campagna et al. 1995; Bennet et al. 2001; Bajzak et al. 2009). We therefore classified each dive according to day-stage (day, night, sunrise, sunset), accounting for spatial position and season. Local times for each dive were calculated according to the associated longitude values of each dive and the appropriate standard time zone (based on UTC). Seasonal local times of sunrise and sunset for 2009 (by latitude) were obtained from the National Oceanic and Atmospheric Administration (NOAA) (http://www.srrb.noaa.gov/highlights/sunrise/sunrise.html). Local-time hour values of dives, season and local times of sunrise/sunset were then used to classify the day-stages of individual dives.

To account for the potential influences of sea ice on individual dive behaviour, we further removed all dive data collected at latitudes higher than 60°S. Data used in the models were therefore restricted to dives with positive bottom dive residuals, completed at latitudes lower than 60°S.

Statistical analyses and model selection

All parameters presented were summarised to daily mean values per track. This was done to smooth out potential biases associated with unsuccessful transmissions of dive profiles (Vincent et al. 2002; Boehme et al. 2009), and potential biases in the likelihood of successful transmissions associated with geographic positions and the orbit of Argos satellites (Argos 1996). Daily mean values further allowed for modelling of temporal autocorrelation, using functions that were computationally too intensive to use on raw data (see below).

Maximum dive depths (MD_{DAY} / MD_{NIGHT}), dive durations (DD_{DAY} / DD_{NIGHT}) and exploited depths (ED_{DAY} / ED_{NIGHT}) were compared with linear mixed-effects models (LMEs). Three covariates were considered in the models: sex, start age (age of animals at the time of deployment) and standard length. These were included in the models as fixed effects, and individual tracks as a random effect. Restricted maximum likelihood (REML) estimation was employed in all model fits, following Bolker et al. (2009).

Autocorrelation plots revealed significant temporal autocorrelation evident in all models. We therefore modelled temporal autocorrelation dependencies, by including autoregressive functions (Pinheiro & Bates 2004; Crawley 2007). Final model covariates were chosen using backwards selection, starting with the 3 covariates models. We used second order Akaike's information criterion (AIC) statistics for small sample sizes (Burnham & Anderson 2002) to govern initial model selection, along with various plot types to asses model fits (Pinheiro & Bates 2004). Hypothesis tests (*F* tests) were carried out on the final models to distinguish significance of the various fixed effects (Bolker et al. 2009). Variance components analyses were also carried out on the final mixed-effects models to estimate the variation explained by random effects (individual) (Börger et al. 2006; Crawley 2007; Bunnefeld et al. 2009).

Models were run using R version 2.7.1 (R Development Core Team 2008). The significance level for all tests was set at $p \leq 0.05$.

Results

Male and female animals in our study travelled in similar directions from Marion Island, predominantly travelling in western and south-western directions (Fig. 5.1a). MCPs indicated substantial overlap in total areas utilised between sexes. Fifty percent kernel density estimates indicated less overlap between the sexes, though these areas were in similar regions (Fig. 5.1b). Males appeared to concentrate their movements in closer proximity to Marion Island than females. Bottom depth estimates (Smith & Sandwell 1997) of the individual dive locations indicated substantial overlap in bottom depths between sexes, though males tended to dive in areas with slightly shallower water depths than females (males: 3 523 ± 1 622 m; females: 4 399 ± 851 m) (Fig. 5.2).

The 20 tracks resulted in 99 302 dives that were successfully transmitted. The filtering process removed 5 090 dives, resulting in 94 212 dives remaining for analyses. Of these, 72 794 dives had calculated bottom times greater than 0, and were used to calculate bottom time residuals. After removal of dives located at latitudes higher than 60°S, daily averaging resulted in 2 810 ‘dive days’ and 2 924 ‘dive nights’.

Start age was not significantly correlated with standard length (Pearson: $r = 0.24$, $df = 18$, $p = 0.31$), and standard length was not significantly correlated with sex (Pearson: $r = 0.41$, $df = 18$, $p = 0.07$) in our study animals. While backwards selection was employed, models were always run with all possible combinations of fixed variables. Models including each of the fixed variables provided the best fit to the dataset for each of the dive parameters in our study (Table 5.2).

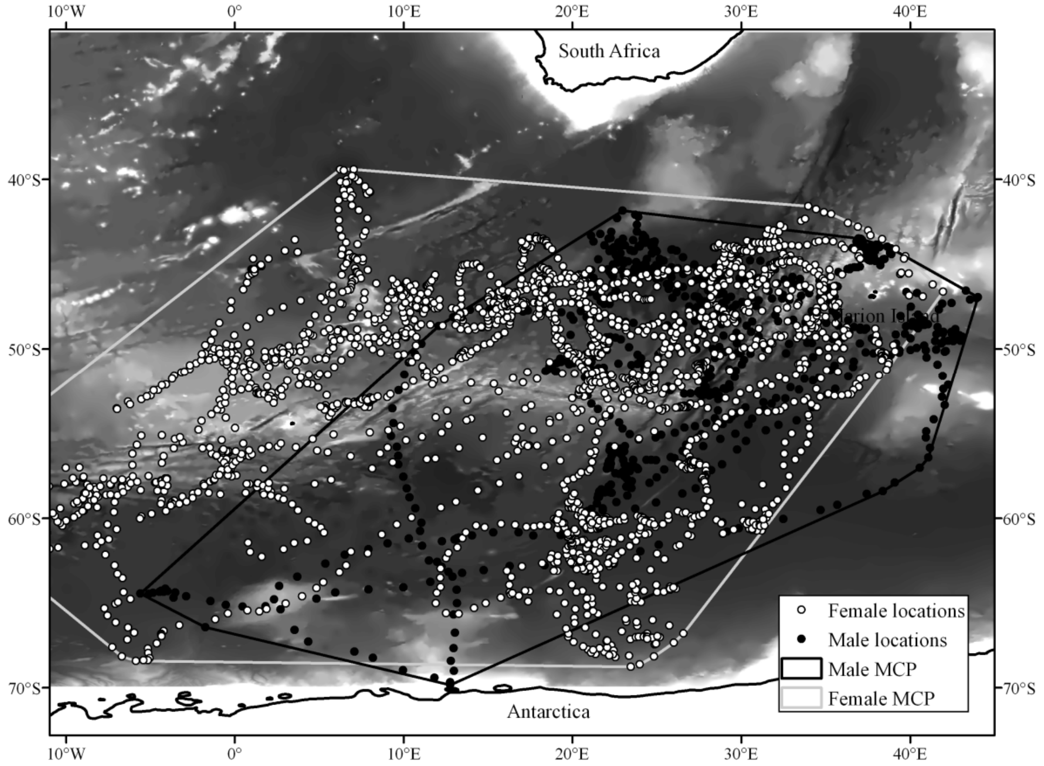

Figure 5.1a: Daily averaged dive locations of the 20 animals (8 males; 12 females) tracked in this study. Minimum convex polygons (MCPs) of their track data are indicated. Background shading indicate the underlying bathymetry (dark shading = deeper water; light shading = shallower water).

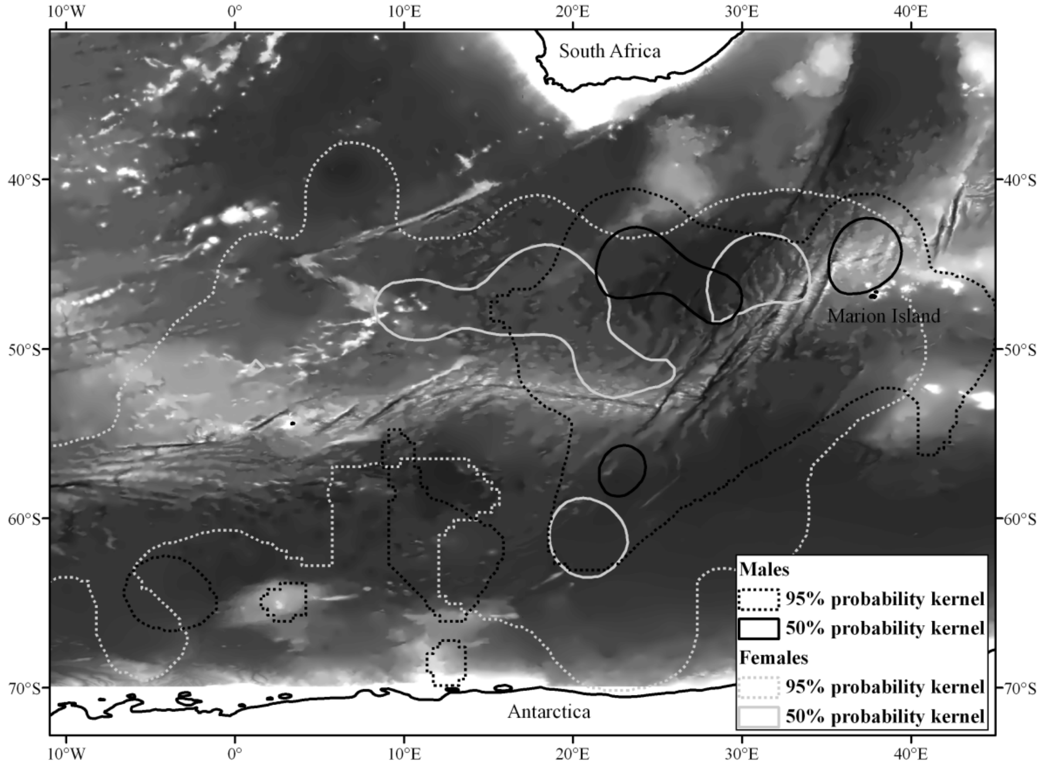

Figure 5.1b: Kernel density estimates of the 20 (8 males; 12 females) southern elephant seal tracks included in this investigation.

Table 5.2: Summary of models with best fits. Models without an asterisk (*) are final models prior to the inclusion of an autocorrelation function. Models with an asterisk (*) indicate final models that included an autoregressive autocorrelation function. DD = dive duration; MD = maximum dive depth; ED = exploited dive depth; stdl = standard length; AIC_c = second order AIC statistic; and RE = random effect.

Parameter	Model	AIC_c	Significant effects	RE (%)
DD_{DAY}	sex + start age + stdl	43 569.4	stdl	29.4
	sex + start age + stdl*	41 460.4	stdl	16.5
DD_{NIGHT}	sex + start age + stdl	43 522.4	start age + stdl	19.2
	sex + start age + stdl*	41 835.7	start age + stdl	12.9
MD_{DAY}	sex + start age + stdl	35 113.9	stdl	43.7
	sex + start age + stdl*	34 040.3	sex + stdl	38
MD_{NIGHT}	sex + start age + stdl	37 125.6	sex	16.3
	sex + start age + stdl*	36 158.8	sex	11.1
ED_{DAY}	sex + start age + stdl	34 911.1	stdl	44.4
	sex + start age + stdl*	33 880.9	sex + stdl	39
ED_{NIGHT}	sex + start age + stdl	36 754.8	sex	17.9
	sex + start age + stdl*	35 849.1	sex	12.8

Maximum dive depths

Males dived to deeper mean maximum dive depths than females, and both sexes dived to deeper mean depths during daytime, when compared to night-time dives ($Males_{DAY}$ = 663.6 ± 186 m; $Males_{NIGHT}$ = 466.8 ± 196.58 m; $Females_{DAY}$ = 548.5 ± 138 m; $Females_{NIGHT}$ = 382.3 ± 140.8 m). Males displayed more variation in maximum dive depths than females (Fig. 5.3). Maximum dive depths were rarely constrained by estimated water depths, and few evident benthic dives were observed in either sex (Fig. 5.4). Sex and standard length significantly affected maximum dive depths during the day, while sex was the only fixed effect influencing maximum dive depths at night in the final models (Table 5.2 and 5.3). Individual track (random effect) explained 38% of the variance in the final model for MD_{DAY} and 11.1% of the variance in the final model for MD_{NIGHT}.

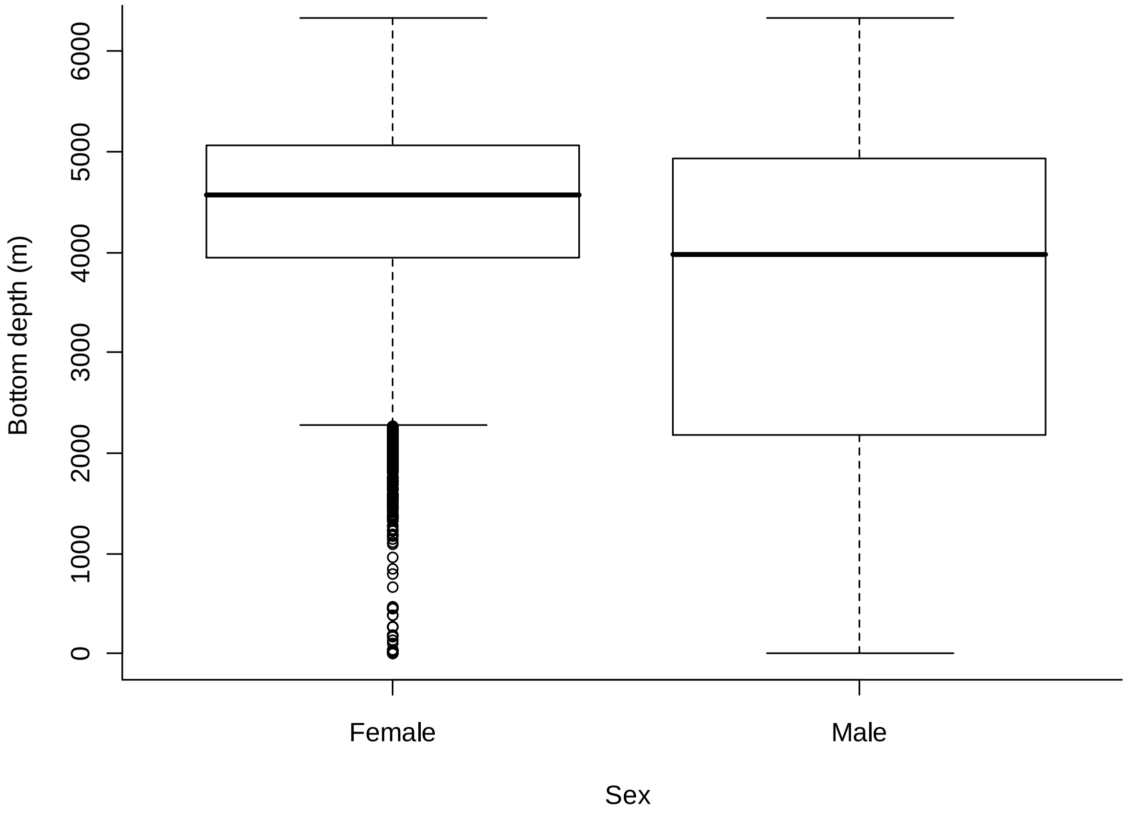

Figure 5.2: Box-and-whisker plot indicating estimated water depths (Smith & Sandwell 1997) of dive locations recorded for the selected southern elephant seal tracks in this investigation. Bold line = median, box = 25th and 75th percentiles, points = outliers, whiskers = 1.5 times the interquartile range, or the maximum values (when there are no outliers).

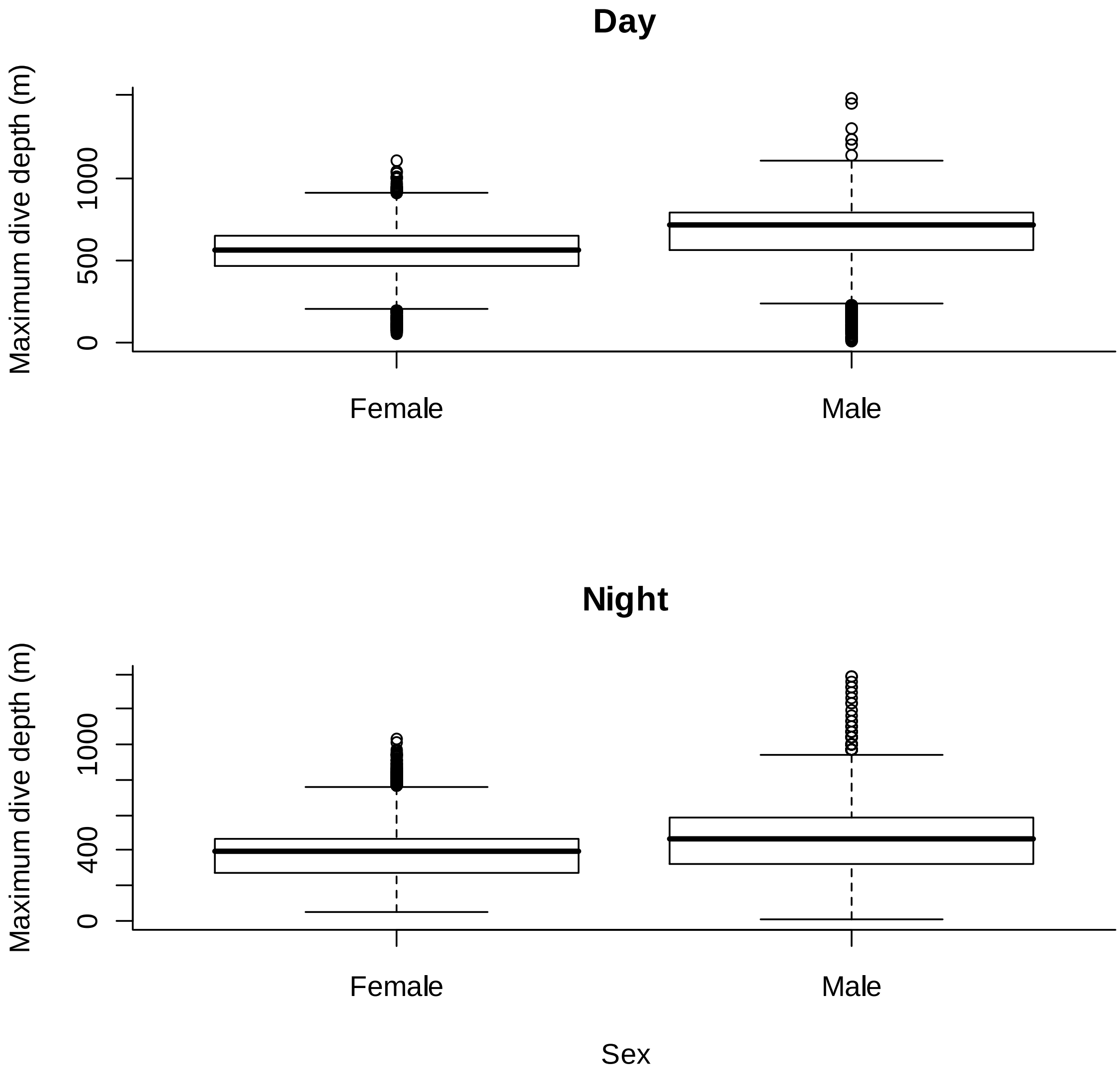

Figure 5.3: Box-and-whisker plots of maximum dive depths obtained by animals in the selected tracks. For definition of box plots see Fig. 5.2.

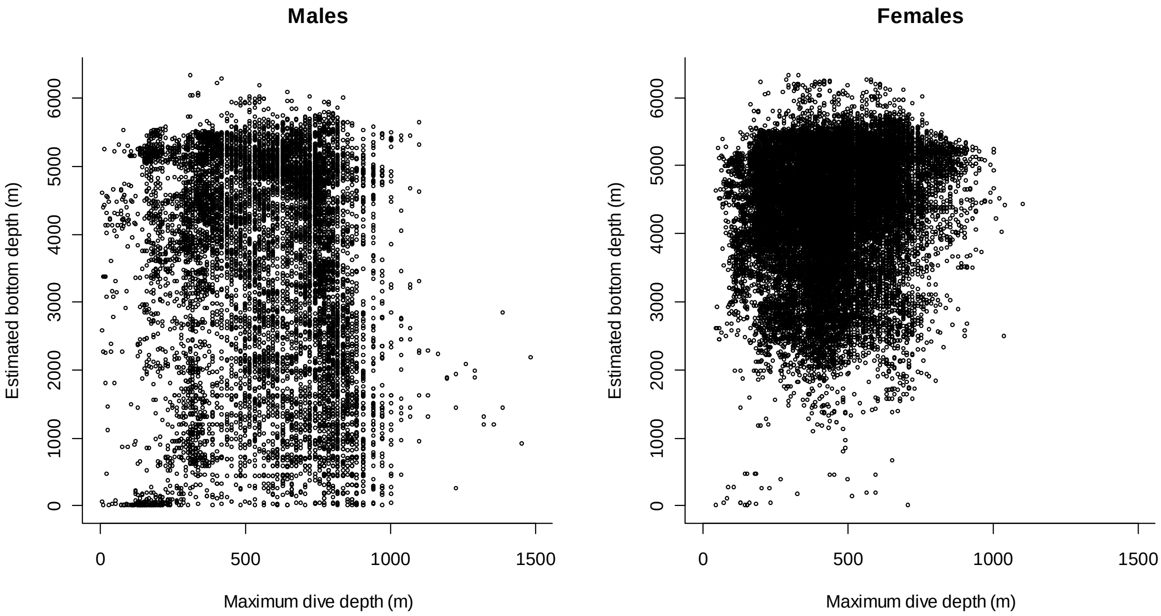

Figure 5.4: Scatterplots of maximum dive depths and estimated bottom depths. Estimates of bottom depths were derived from Smith & Sandwell (1997).

Dive durations

Dive durations (DD) were longer in males than females, and both sexes dived for longer mean periods of time during the day than during night-time dives (Males$_{DAY}$ = 35.5 ± 2.8 min; Males$_{NIGHT}$ = 26.2 ± 9.5 min; Females$_{DAY}$ = 31.8 ± 9.7 min; Females$_{NIGHT}$ = 24 ± 7.4 min) (Fig. 5.5). The best model for DD$_{DAY}$ indicated that standard length was the only significant fixed effect influencing this parameter (Table 5.3). A weak, but statistically significant positive correlation existed between DD$_{DAY}$ and standard length (Pearson: $r = 0.31$, df = 2808, $p < 0.001$). Both standard length and start age were identified as significantly influencing DD$_{NIGHT}$. Individual track (random effect) explained 16.5% and 12.9% of the variance in the final models for DD$_{DAY}$ and DD$_{NIGHT}$ respectively.

Table 5.3: *F* test results indicating significant fixed effects on final models. **Boldface** indicates statistically significant effects ($p < 0.05$). DD = dive duration; MD = maximum dive depth; ED = exploited dive depth.

		ANOVA		
Response variable	**Fixed effect**	**F**	**df**	**p**
DD_{DAY}	**intercept**	**924.124**	**1,2790**	**< 0.001**
	sex	1.131	1,16	0.303
	start.age	0.002	1,16	0.969
	stdl	**10.909**	**1,16**	**0.005**
DD_{NIGHT}	**intercept**	**1328.123**	**1,2904**	**< 0.001**
	sex	1.761	1,16	0.203
	start.age	**6.58**	**1,16**	**0.021**
	stdl	**9.933**	**1.16**	**0.006**
MD_{DAY}	**intercept**	**651.932**	**1,2790**	**< 0.001**
	sex	**4.762**	**1,16**	**0.044**
	start.age	0.018	1,16	0.894
	stdl	**4.752**	**1,16**	**0.045**
MD_{NIGHT}	**intercept**	**1162.961**	**1,2904**	**< 0.001**
	sex	**13.609**	**1,16**	**0.002**
	start.age	1.028	1,16	0.326
	stdl	0.234	1,16	0.635
ED_{DAY}	**intercept**	**587.416**	**1,2790**	**< 0.001**
	sex	**4.502**	**1,16**	**0.05**
	start.age	0.006	1,16	0.939
	stdl	**5.374**	**1,16**	**0.034**
ED_{NIGHT}	**intercept**	**931.25**	**1,2904**	**< 0.001**
	sex	**10.572**	**1,16**	**0.005**
	start.age	1.189	1,16	0.292
	stdl	0.267	1,16	0.612

Exploited dive depths

Exploited dive depths were deeper in males when compared to females, and deeper during daytime dives when compared to night-time dives for both sexes (Males_{DAY} = 622.2 ± 185.8 m; Males_{NIGHT} = 416.6 ± 186.4 m; Females_{DAY} = 511.2 ± 134.1 m; Females_{NIGHT} = 342.5 ± 136.6 m). Males displayed more variation in exploited dive depths than females (ANOVA_{DAY}: $F_{1,17230}$ = 2 020.8, $p < 0.001$; ANOVA_{NIGHT}: $F_{1,18514}$ = 892.77, $p < 0.001$; Fig. 5.6). Best models for exploited depth indicated that sex and standard length significantly influenced exploited dive depths during day-time dives (Table 5.3). Sex was identified as the only fixed effect significantly influencing exploited depths at night. Individual track (random effect) explained 38.9% of the variance in the final model for ED_{DAY} and 12.8% of the variance in the final model for ED_{NIGHT}.

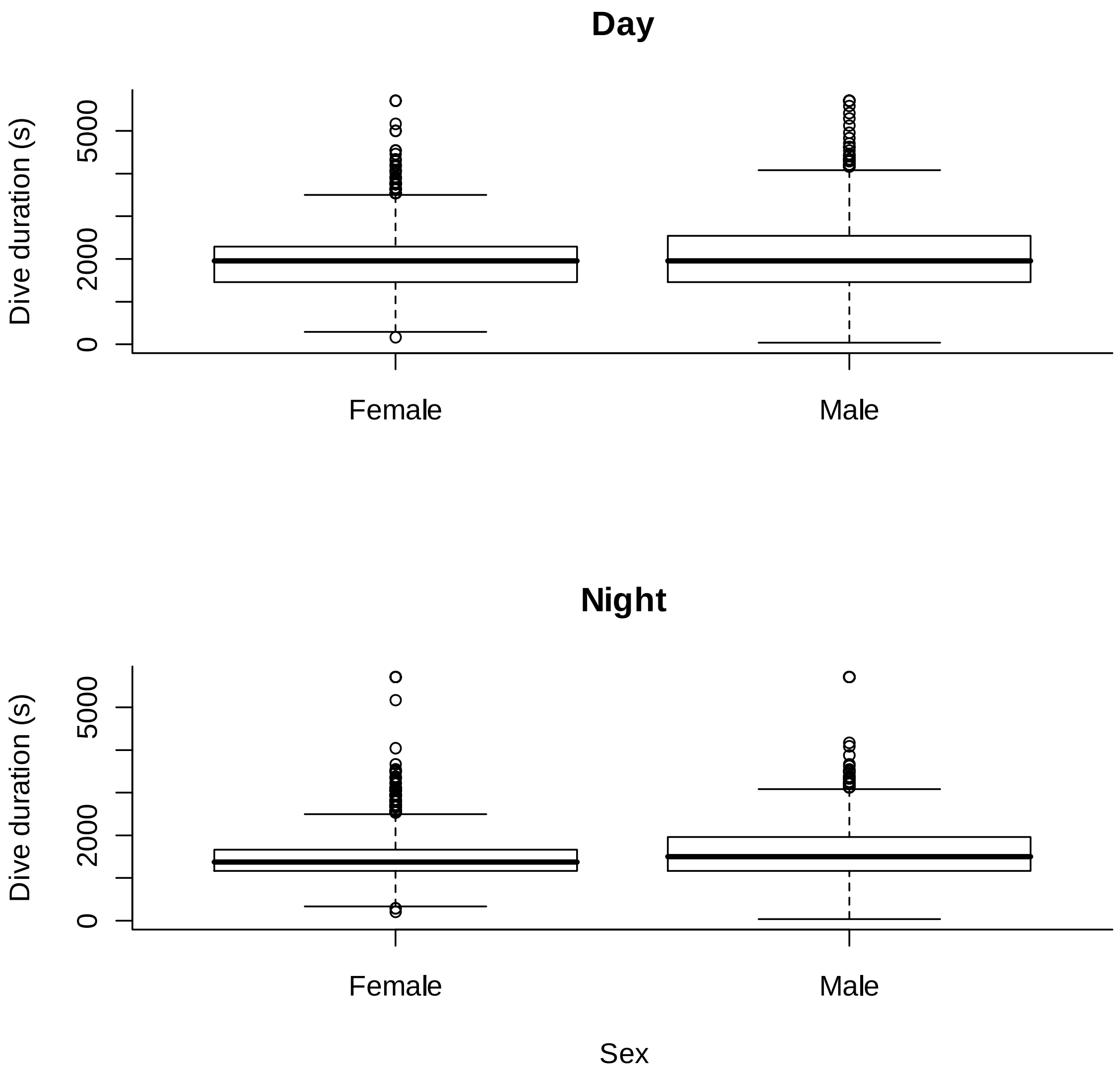

Figure 5.5: Box-and-whisker plots of dive durations recorded for the southern elephant seal tracks selected for this investigation. For definition of box plots see Fig. 5.2.

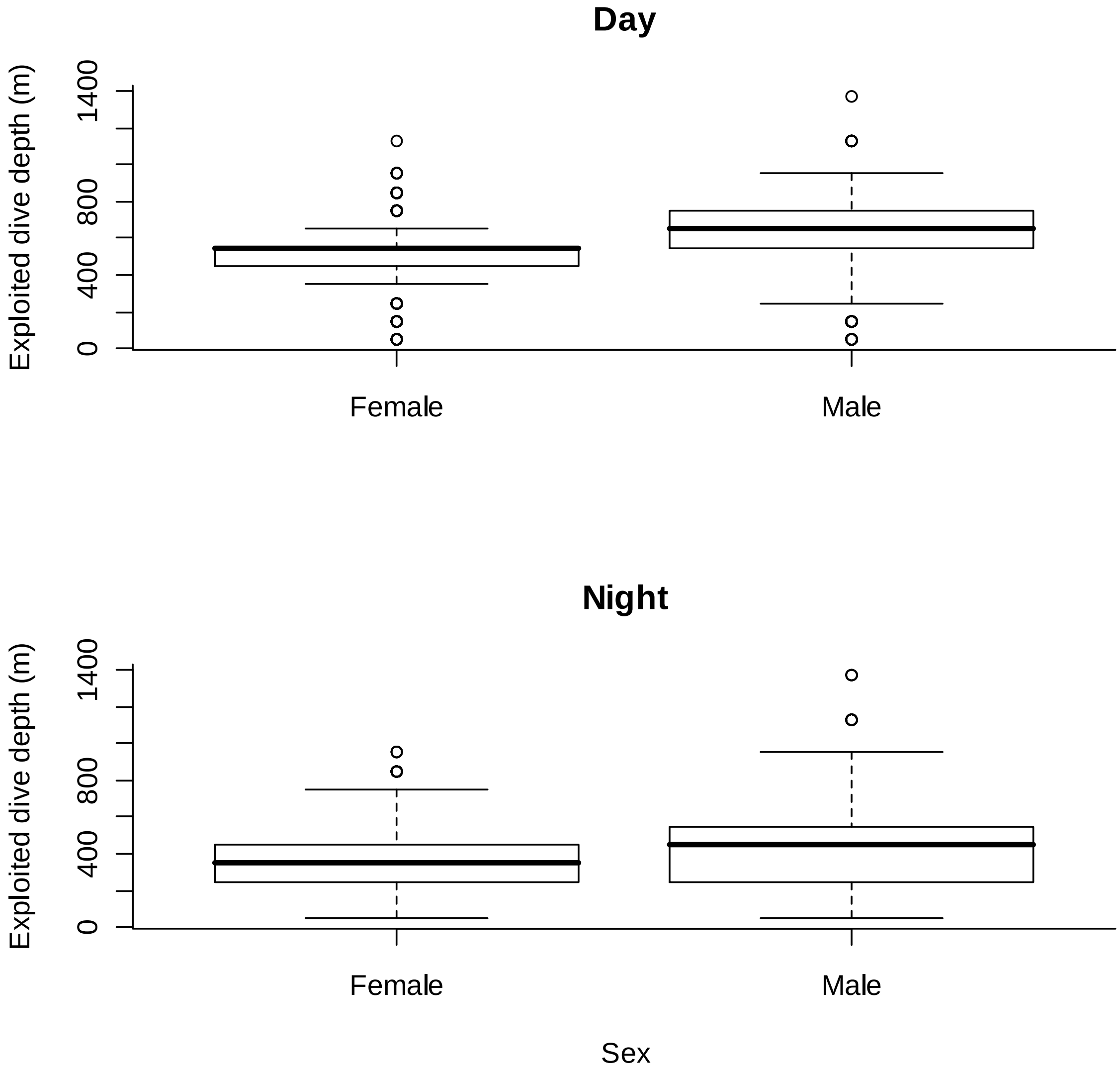

Figure 5.6: Box-and-whisker plots of exploited dive depths of southern elephant seal tracks selected for this study. For definition of box plots see Fig. 5.2.

Discussion

This study investigated the effects of sex, size and age on a number of dive parameters measured in southern elephant seals from Marion Island. By examining track and dive data obtained from seals from a range of sizes (standard lengths) in each sex, we were able to elucidate the influence of such effects using a mixed-effects modelling approach.

Sex vs. Size

Males in our sample undertook longer and deeper foraging dives than females - dives characterised by increases in time spent at the bottom of dives. Male southern elephant seals displayed more variation in maximum and exploited dive depths than females (Figs. 5.3 and 5.6). Sex was considered a significant effect in final models for maximum dive depth and exploited dive depth during day- and night-time. However, sex did not have a significant effect in final models for dive duration. Standard length was incorporated in the best models for all dive parameters. It was identified as being a statistically significant effect for dive durations during day- and night-times, as well as daytime maximum and exploited dive depths. While the inclusion of standard length improved all final models, it was not identified as a significant effect for maximum or exploited depths at night.

These results suggest that differences observed in dive durations between sexes are likely to be due largely to increased physiological capability associated with different body sizes. Swim speed and body mass have previously been reported to be positively correlated with dive durations in female southern elephant seals from Macquarie Island (Irvine et al. 2000). Similarly, a positive relationship between body mass and dive durations were reported for underyearling southern elephant seals from the same population (Irvine et al. 2000).

However, body size (standard length) did not appear to drive differences observed between sexes in maximum and exploited dive depths. While body size significantly influenced both these parameters for day-time dives, sex was identified as consistently affecting maximum- and exploited dive depths during day- and night-time dives. This suggests that male and female southern elephant seals target different depth layers and their associated resources due to differences in foraging strategy, and that dive depths are not merely a by-product of body size and their associated physiological capacity.

We used standard length as a proxy measurement for body size. While such a measurement was not sufficient to estimate body condition in the study animals, it was considered likely to provide an overall indication of physiological capability over an extended time scale. Body condition in southern elephant seals is known to vary substantially during their foraging migrations and over seasonal timescales (Bennet et al. 2001; Biuw et al. 2007).

Such changes in body condition can be expected to directly influence dive performance due to changes in buoyancy associated with blubber gain and loss. Other seasonal influences on dive performance have been suggested, including reproductive condition of females; seasonal fluctuations in basal metabolic rate; seasonal alterations in oxygen affinity of haemoglobin and myoglobin; increases in muscle oxygen storage capacity; increases in physical fitness; and seasonal changes in prey type (Bennet et al. 2001). Such factors are likely to have resulted in the large variances in dive parameters reported here, and require further investigation. Furthermore, differences in metabolic requirements between males and females of similar ages (non-breeding males provisioning for growth and females for breeding) (Field et al. 2005a) were likely to have resulted in different body conditions and dive performances between sexes.

The influence of age

Dietary shifts associated with age have previously been described for juvenile southern elephant seals (Field et al. 2007b; Bailleul et al. 2010a). We therefore expected age to exhibit significant influences on maximum and exploited dive depths. Surprisingly, age was only identified as being a statistically significant fixed effect in one of the models selected (DD_{NIGHT}), though it was always included as a contributing effect in the model structures. Since we selected the sample of animals to obtain a sufficient overlap in standard lengths between sexes, the study was limited to individuals of ages between 2 yr, 6 mo and 8 yr, 4 mo. We therefore did not include any dive data from underyearlings or yearlings – ages at which dietary changes associated with increased dive capacity would perhaps be most evident. Indeed, stable isotope ratios indicate that young males from the Kerguelen Islands show an increase in foraging trophic level from approximately 3 to 4 yr of age (Bailleul et al. 2010a). The exclusion of very young and older adult animals (this study) probably also resulted in the lack of correlation between age and standard length in our study sample.

Individual variation in dive behaviour

Individual variation explained large proportions of the total variance in many of the final models selected in this study (11.1 – 39%). The influence of individual variation declined in all models after inclusion of the autoregressive correlation functions. Individual track variation explained more of the model variance for all daytime dive behaviour models, than for night-time models. Slight increases in variation were evident in most night-time dive behaviour parameters, when compared to daytime dive behaviour (Figs. 5.3, 5.5 and 5.6), though this variation did not appear sufficient to clarify the differences in variance explained by individual tracks between day- and night-time dives.

Individual variation potentially plays a significant role in the behaviour of various animal taxa (Bolnick et al. 2003), and has previously been reported in dive behaviour of southern elephant seals (Field et al. 2001) and other pinnipeds (Staniland et al. 2004; Chilvers & Wilkinson 2009; Kuhn et al. 2009). Individual variation has often been ascribed to the influence of dive localities however, and the associated bathymetry and prey distribution on an individual's behaviour. Our results did not provide support for any particular explanation for the influence of individual variation in our sample. However, while we acknowledge the likely influence of localised conditions and prey distribution on the dive behaviour of individuals, some differences in individual strategy appear to be evident (McIntyre unpublished data).

The smaller amount of variation explained by the effect of individual for night-time dive parameters suggest that southern elephant seals perhaps use less specialised strategies for night-time foraging purposes. This in turn, could be the result of prey resources displaying less patchy distributions at night, and concentrating their activity in shallower water layers (Collins & Rodhouse 2006; Collins et al. 2008).

Diel variation and diet

Southern elephant seals prey largely on squid and myctophid fishes (Bradshaw et al. 2003; van den Hoff et al. 2003), though substantial inter-population and seasonal differences in diet have been documented (Bradshaw et al. 2003; Cherel et al. 2008). Comparatively little is known about the diet of southern elephant seals hauled out at Marion Island. Diel variation in all dive parameters measured was evident in the sample of tracks investigated. Males and females dive to deeper depths for longer periods of time during daytime dives, than during night-time dives (Figs. 5.3, 5.5 and 5.6). Such variation suggests that both male and female southern elephant seals target vertically migrating, pelagic prey species (Hindell et al. 1991; Jonker & Bester 1994; Bost et al. 2002), though males evidently target prey occurring at deeper depths than females (Fig. 5.3). Dive depths were rarely constrained by estimated bottom depths and very few benthic dives were recorded in our sample. This is not surprising, given the deep water immediately surrounding Marion Island, and that seals from this population evidently do not often target large areas of shallow bathymetry (e.g. continental shelves). Our results differ from those reported for other populations, notably Peninsula Valdés (Campagna et al. 1999), Kerguelen Islands (Bailleul et al. 2007a; 2010a) and Macquarie Island (Hindell et al. 1991), where males often forage benthically over continental and oceanic shelves. The different foraging strategy reported here for males from Marion Island highlights the evident foraging plasticity between populations of this species.

Resource selection and partitioning

The avoidance of intra-specific competition between sexes, as well as age-classes has previously been proposed to drive resource partitioning in southern elephant seals (Lewis et al. 2006; Field et al. 2007a; Newland et al. 2009). While elephant seals from other populations segregate spatially between the sexes (Slip et al. 1994; Campagna et al. 1995; 1999; Bornemann et al. 2000; Tosh et al. 2009; Bailleul et al. 2010a), animals from Marion Island appear to largely segregate between the sexes by targeting different water depths in oceanic environments.

Our results suggest that both sex and body length play important roles in the dive behaviour of southern elephant seals from Marion Island. Segregation between the sexes was evident in the vertical depth layers targeted by animals of either sex – males diving deeper than females, and also evidently exploiting increased depths. The dive depths obtained and targeted by animals were evidently not constrained by physiological capacity (associated with body size), but rather selected by the individual animals. This provides support for a hypothesis that segregation in dive depths of southern elephant seals is largely driven by forage selection and an associated avoidance of intra-specific competition.

The comparative lack of influence that sex exhibited on dive durations in this investigation further indicated that the physical size of animals did not govern the depths utilised, but rather the amount of time seals were able to spend at targeted depths. This result supports previous investigations that highlighted a positive correlation between body size and maximum dive durations (Hindell et al. 2000; Irvine et al. 2000).

Conclusion

We presented results from mixed-effects models to elucidate the effects of sex, age and size on the dive behaviour of a highly sexually dimorphic mammal, the southern elephant seal. While individual variation accounted for substantial portions of variance in the models, differences in maximum and targeted depths were always influenced by sex, and only partly influenced by body length. Conversely, dive durations were always influenced by body length while sex was not identified as a significant influence. These results support previous investigations where physiological capability associated with size was hypothesised as being a limiting factor on dive durations (Hindell et al. 2000; Irvine et al. 2000). However, our results suggest that sexual segregation in vertical depth use (i.e. maximum and exploited dive depths) by southern elephant seals is largely a result of forage selection, and not a result of size differences between sexes. This provides support for resource partitioning between sexes and the potential avoidance of intra-specific competition in this species (Field et al. 2007a). Furthermore, inter-population differences in sexual segregation (i.e. by using different water depths in pelagic habitats or by utilising different spatial foraging habitats) highlight the plasticity in forage strategies of southern elephant seal populations.

CHAPTER SIX: OCEAN WARMING AND THE DIVE BEHAVIOUR OF A TOP PREDATOR: DIVING CLOSER TO THE EDGE?*

Abstract

The potential effects of ocean warming on top predators are largely unknown, though the impact on the distribution of prey in vertical space may have far reaching impacts on diving predators such as southern elephant seals. We used data from satellite-tracked southern elephant seals from Marion Island to investigate the relationship between their dive characteristics (dive depths, dive durations and time-at-depth index values) and environmental variables (temperature at depth, depth of T_{max} below 100m, frontal zone and bathymetry) as well as other demographic and behavioural variables (migration stage, age-class, track day and vertical diel strategy). While other variables, such as bathymetry and vertical diel strategy influenced dive depth, our results also consistently indicated a significant influence of temperature at depth on dive depths. This relationship was positive for all groups of animals, indicating that seals dived to deeper depths when foraging in warmer waters. Female seals adjusted their dive depths proportionally more than males in warmer water. Dive durations were also influenced by temperature at depth, though to a lesser extent. Results from time-at-depth indices showed that both male and female seals spent less time at targeted dive depths in warmer water, and were presumably less successful foragers when diving in warmer water. Continued warming of the Southern Ocean may result in the distribution of prey for southern elephant seals shifting either poleward and/or to increasing depths. Marion Island elephant seals are expected to adapt their ranging and diving behaviour accordingly, though such changes may result in greater physiological costs associated with foraging.

* Submitted for publication as: McIntyre, T., Ansorge, I.J., Bornemann, H., Plötz, J., Tosh, C.A. & Bester, M.N. (under review) Ocean warming and the dive behaviour of a top predator: diving closer to the edge? *Marine Ecology Progress Series*

Introduction

The world's oceans are warming and are likely to continue this trend as climate impacts become more pronounced (Levitus et al. 2000; Solomon et al. 2009). The Southern Ocean in particular is warming. Recent studies have shown that, since the 1950's, the Antarctic Circumpolar Current (ACC) has strengthened and migrated southwards by 50-70km, resulting in an increase in global ocean temperatures in the upper 1 000m (Gille 2002). This warming has further been linked to changes in wind stress, which has shown a southward expansion of the Southern Hemisphere westerlies over a 30-yr period (Large & Yeager 2004), thereby influencing the Southern Ocean eddy field and its contribution to the poleward heat flux (Meredith & Hogg 2006). Indeed, hydrographic data collected north of the Prince Edward Islands for the period 1959 to 1999 indicate a positive trend in the southward migration of the Subantarctic Front (SAF) (Pakhomov & Chown 2003; Ansorge et al. 2009). The most rapid warming appears to be concentrated along the Subantarctic Belt (Le Roux & McGeoch 2008) and at the SAF (Gille 2002). Such changes in water temperature are causing complex changes in marine ecosystems across the world, notably changes in species' geographic distributions accompanied by simultaneous changes in vertical distribution (Perry et al. 2005; Dulvy et al. 2008; Nye et al. 2009). The effects of such climate changes on marine mammals may be direct (e.g. through loss of habitat from sea-ice breakup (Ferguson et al. 2005)), or indirect (e.g. through changes in prey availability and distribution, susceptibility to diseases etc. (Learmonth et al. 2006; Simmonds & Isaac 2007)).

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The distribution of prey species in time and space influences the dive behaviour of marine mammals, especially pinnipeds (Hindell et al. 1991; Harcourt et al. 2002). Southern elephant seals (*Mirounga leonina*) are top predators in the Southern Ocean and have a circumpolar distribution (Le Boeuf & Laws 1994b). Links have previously been explored between population demographics of the species and climatic changes, suggesting that first year survival may be affected by changes in oceanographic conditions related to the El Niño Southern Oscillation (ENSO) (McMahon & Burton 2005). The distribution and dive behaviour of elephant seals has also been related to oceanographic conditions. Some southern elephant seals from the Kerguelen Islands tend to focus their forage efforts on zones with specific temperature signatures (Bailleul et al. 2007b). Female southern elephant seals from

Macquarie Island apparently do not alter their dive behaviour in response to changes in thermal structure, though differences in dive behaviour are evident as seals move between different water bodies (Field et al. 2001). Broader-scale assessments have described associations of forage locations with inter-frontal zones (Jonker & Bester 1998; van den Hoff et al. 2002), continental shelves and areas close to the Antarctic ice edge (Bornemann et al. 2000; Biuw et al. 2007; Tosh et al. 2009), as well as mesoscale features such as eddies (Bailleul et al. 2010b; Dragon et al. 2010). The use of oceanographic data collected *in situ* by animal-borne devices may further enhance our understanding of diving responses to oceanographic conditions.

Marion Island (46° 54’S; 37° 45’E) is one of two islands that together form the Prince Edward Islands (PEI). Southern elephant seals from Marion Island forage over a wide area of the Southern Ocean that stretches from the Antarctic shelf in the south to areas north of the SAF in the north (Jonker & Bester 1998; Tosh 2010). Animals typically return to the island twice a year, for giving birth, nursing pups and mating during the austral spring, and again for moulting later in the austral summer (Le Boeuf & Laws 1994b). This results in two forage migrations per year, a post-moult (PM) trip lasting up to nine months, and a shorter post-breeding (PB) trip of approximately three months. The Marion Island population is one of the northernmost breeding colonies and its animals are extreme divers that spend more than 65% of their lives at sea in depths deeper than 100 m (chapter 2). Although short-term variability (i.e. changes in eddy intensity or frequency) cannot be completely discounted, there is strong evidence that sea temperatures close to the islands continue to rise (Mélice et al. 2003) and top predators from PEI are considered likely to be influenced significantly by such warming. Here we used temperature data recorded *in situ* to model the influences of temperature at depth and other variables on the dive behaviour of Marion Island elephant seals.

Methods

Deployments

We deployed 59 satellite-relay data loggers (SRDLs) (Sea Mammal Research Institute, University of St. Andrews, Scotland) between 2004 and 2008 on southern elephant seals hauled out at Marion Island. Animals were immobilised following Bester (1988a), and

SRDLs glued to the dorsal, cranial pelage as detailed in chapter 2. Two SRDL models were used, namely the Series 9000 SRDL and CTD-SRDL. Series 9000 SRDLs recorded and transmitted, via Service Argos (Argos 1996), abstracted dive profiles and temperature profiles with an accuracy better than 0.01 °C (Boehme et al. 2009). CTD-SRDLs were additionally fitted with a conductivity sensor (Valeport Ltd., Boehme et al. 2009). Location estimates for animals were obtained via Service Argos and interpolated locations attributed to individual dive profiles by the manufacturers (Sea Mammal Research Institute). All dive-, temperature- and conductivity data, as well as the related meta-information are available via the PANGEA information system (http://pangaea.de).

Dives / temperature profiles

We calculated local times and local times of sunset and sunrise for each transmitted dive profile, using the ‘maptools’ package in the R environment (Lewin-Koh & Bivand 2008; Team 2008). Each dive was accordingly labelled as having taken place either during daytime, night-time, or during sunset/sunrise (sunset/sunrise was defined as the period falling within 30 min before and after the calculated time).

Transmitted dive- and temperature profiles do not necessarily correspond temporally or spatially with one another, since information is compressed and stored temporarily in a buffer onboard the SRDLs prior to transmission (Boehme et al. 2009). We therefore calculated daily averaged values of various dive parameters and temperature profiles in order to make them comparable and further to eliminate potential biases due to variable uplink rates. To account for expected difference in dive characteristics between different oceanographic zones, we assigned each dive day to a frontal zone based on the averaged location of uplinks received for the particular day and estimated frontal positions following Belkin & Gordon (1996). Accordingly daily locations were classified as either occurring north of the Subantarctic Front (SAF), between the SAF and the Antarctic Polar Front (APF), or south of the APF.

Elephant seals from Marion Island have been documented to display positive, as well as negative diel vertical migration (i.e. positive = diving deeper during the day compared to night-time; negative = diving deeper at night compared to daytime) patterns in dive depths whilst foraging pelagically (chapters 3 and 4). A diel vertical strategy (DVS) was therefore assigned to each dive day. Accordingly, seals were considered to make use of a positive diel vertical strategy if the difference between mean dive depths during the day (-SE) and mean dive depths at night (+SE) exceeded 25 m. If this difference was smaller than -25 m (i.e. the seal dived substantially deeper at night, compared to during the day) a negative diel strategy was attributed, and if this difference was between -25 m and 25 m the seal was considered to make use of a neutral diel strategy. A cut-off value of 25 m was chosen as representing a value of approximately 5% of the mean dive depths of southern elephant seals from this population (chapter 2).

A time-at-depth index (TAD) was calculated following Fedak et al. (2001), providing a depth and duration independent index, indicating the relative depth where an animal centred its activity. Accordingly, values close to 1 are indicative of an animal maximising the amount of time close to the maximum depth of a dive. Values approaching 0.5 are indicative of an animal spending more or less equal amounts of time at all recorded dive depths and values closer to 0 are obtained when an animal spends most of the dive time close to the sea surface and only makes a short excursion to the maximum depth recorded. Since elephant seal dives can be classified into various “types”, based on their time-depth characteristics (Hindell et al. 1991; Jonker & Bester 1994; Biuw et al. 2007), we restricted the daily averaged TAD values to specific dive types thought to have a foraging purpose. For classifications of dives we used a method that employs Breiman’s random forest (RF) algorithm (Breiman 2001) to classify each dive into one of six recognized types, namely square (SQ), root (R), drift (DR), U-shaped (U), V-shaped (V), and wiggle (W) dives (see Photopoulos 2007; chapter 3 (this thesis)). A total of 18 derived variables were used for the RF classification. The RF tree-building method was employed using the “randomForest” package in R (Liaw & Wiener 2002). We restricted the calculations of averaged TAD values to U- and W-shaped dives. SQ dives were not included in our analyses, since they made up a very small proportion (< 1%) of dives classified. We further calculated the daily ratio of U- and W-shaped dives (combined) as a proxy for frequency of forage-type diving. A summary of derived dive- and temperature parameters is provided in Table 6.1.

Table 6.1: Descriptions of parameters used in mixed-effects models.

Parameter	**Description**	
Fixed variables		
Tday	Trackday: day number since start of track	
Age class	Females:	Subadults (younger than 3 yrs) Adults (older than 3 yrs)
	Males:	Subadults (younger than 6 yrs) Adults (older than 6 yrs)
Migration	Migration stage:	Post-moult (i.e. approx. Feb - Oct) Post-breeding (i.e. approx. Nov - Dec/Jan)
Bottom depth	Interpolated depth estimates obtained from the Gebco Digital Atlas (IOC et al. 2003)	
DS	Diel strategy:	Positive (difference between day- and night-time dive depths greater than 25m) Negative (difference between day- and night-time dive depths smaller than -25m) Neutral (difference between day- and night-time dive depths between -25 and 25m)
T_{max}100	Mean maximum temperature recorded at depths deeper than 100m (℃)	
T_{max}100.depth	Mean depth at which T_{max} was recorded (m)	
Response variables		
TAD	Time-at-depth index	Mean TAD value, calculated following Fedak et al (1992)
MeanDDEP.day	Mean dive depths obtained during daytime (m)	
MeanDDEP.night	Mean dive depths obtained during night-time (m)	
MeanDDUR.day	Mean dive durations during daytime (s)	
MeanDDUR.night	Mean dive durations during night-time (s)	

Temperature profiles were inspected visually in Ocean Data View (Schlitzer 2002) and unrealistic or incomplete profiles removed. Profiles were considered unrealistic when they contained extreme outlying values (< -3°C or > 15°C) and/or values within the same profile that differed by more than 40% from preceding and subsequent values. Most of the temperature profiles obtained in the Southern Ocean are characterised by a maximum temperature (T_{max}) layer occurring relatively close to the surface (Pollard et al. 2002). Since southern elephant seals spend more than 80% of their time at sea at depths deeper than 100 m (chapter 2), we calculated the maximum temperature recorded at depths exceeding 100 m (T_{max}100) for each of the recorded temperature profiles. These values were then averaged to obtain daily averaged T_{max}100 values, as well as mean depth values where the T_{max}100 was recorded (T_{max}100.depth). Temperature characteristics at depth were assumed not to differ significantly between day and night.

Dive durations recorded by the female elephant seals in our sample generally increased initially during migrations, and was followed by a decrease from approximately 150 days into the migration, prior to returning to Marion Island. We therefore restricted the females' dive duration data used in the linear mixed models (see below) to data obtained within the first 150 days of individual migrations to satisfy model assumptions. Mean dive depths recorded for male seals were log-transformed to account for very deep dives recorded by one seal in the sample (see chapter 2).

Statistical analyses

We used linear mixed effects models to model the influences of age class, migration stage (PM or PB), track day (TDAY), frontal zone of dive location (FZ: north of SAF; between SAF and APF; or south of APF), bathymetry (seafloor depth), diel vertical strategy (DVS), $T_{max}100$ and $T_{max}100$.depth on various dive parameters (dive depth, dive duration and TAD). Dive depths and dive durations were separated by day-stage (night and day) to account for expected differences in values due to diel vertical migration (Jonker & Bester 1994; Bennet et al. 2001). Since southern elephant seals are known to segregate sexually in depth use patterns (chapter 5), we analysed data separately for males and females. Mixed models allow for the unbalanced design resulting from our sample, as well as the explicit modelling of temporal autocorrelation inherent to our data (Pinheiro & Bates 2004; Bolker et al. 2009). They further allow for variance differences between random variables (individual animals in our sample). Maximum likelihood estimation was employed following Bolker et al. (2009).

We employed second order Akaike's information criterion (AIC_c) statistics for small sample sizes (Burnham & Anderson 2002) to govern model selection. Best models were chosen using backward selection starting with full models that included all fixed effects. Various plot types were used to assess model fits (Pinheiro & Bates 2004; Crawley 2007). Hypothesis tests (*F* tests) were carried out on the final models to distinguish significance of the various fixed effects (Bolker 2008; Bolker et al. 2009). We also carried out variance components analyses on the final models to estimate the variation explained by random effects (Bunnefeld et al. 2009).

All statistical analyses were carried out in R version 2.7.1 (R Development Core Team 2008) , with significance set at $p \leq 0.05$. Unless otherwise stated, summary statistics are reported as means ± SD.

ARGO

The ARGO float programme provides an extensive year round dataset of the world's oceans, and in particular provides information in parts of the ocean difficult to map such as the Southern Ocean and the south Indian Ocean (Roemmich et al. 2000; Roemmich et al. 2004). ARGO floats provide high quality temperature and salinity profiles for the top 2 000 m of the ocean, plus mid-depth drift trajectories, every 10 days. ARGO's objective is to build and maintain a 3 000 – float array (Wilson 2000). For this study, quality controlled temperature profiles from ARGO float data were obtained from the Global Marine ARGO atlas (Roemmich & Gilson 2009) for the period March 2004 – 2010.

Results

Early tag failure (within 30 days from deployment) and/or failure of temperature probes on 15 satellite tags, resulted in data being retained from 44 deployments. Eight animals were instrumented multiple times and two instruments continued functioning over two subsequent migrations (PM and PB). This resulted in data being retained for analyses from 46 tracks, resulting from 44 deployments made on 33 individual animals. Females accounted for 27 (PM = 19; PB = 8) of the tracks, while males accounted for 19 (adult males PM = 5; adult males PB = 4; subadult males = 10) of the tracks analysed here. We did not distinguish between age classes for female southern elephant seals, since our sample did not allow for the adequate quantification of subadult female (n = 2) dive characteristics. Summary dive statistics for these tracks are reported in Table 6.2.

Table 6.2: Summary values (mean ± SD) of dive parameters recorded for animals in this study. FOR$_{day}$ and FOR$_{night}$ are the mean (± SD) proportions of dives that were classified as ‘forage-type’ dives (i.e. had time-depth profiles classified as U- or W-shaped).

	Males ($n_{individuals}$ = 15)			**Females ($n_{individuals}$ = 18)**		
	Adults ($n_{individuals}$ = 7)		**Subadults ($n_{individuals}$ = 9)**	**Adults ($n_{individuals}$ = 17)**		**Subadults ($n_{individuals}$ = 2)**
	PM (n_{tracks} = 5)	**PB (n_{tracks} = 4)**	**(n_{tracks} = 10)**	**PM (n_{tracks} = 17)**	**PB (n_{tracks} = 8)**	**(n_{tracks} = 2)**
nDIVES$_{day}$	3 139	4 326	14 417	30 808	7 594	1 389
nDIVES$_{night}$	5 568	2 189	21 698	49 988	5 666	3 134
DDEP$_{day}$ (m)	767.3 ± 327.3	472.8 ± 101.4	669.5 ± 144.7	582.6 ± 120.7	532 ± 97.1	621.2 ± 83.1
DDEP$_{night}$ (m)	560.5 ± 309.1	374.9 ± 87.9	469 ± 150.6	398.6 ± 96.2	363.9 ± 113	432.3 ± 64
DDUR$_{day}$ (min)	38.3 ± 10.4	29.2 ± 4.8	36.5 ± 11	34.3 ± 10.1	24 ± 4.5	34.9 ± 4.5
DDUR$_{night}$ (min)	30.7 ± 8	24.4 ± 5	26.7 ± 9.1	25.4 ± 7.3	16.3 ± 3	24.5 ± 3.6
FOR$_{day}$	0.91 ± 0.19	0.97 ± 0.04	0.94 ± 0.1	0.96 ± 0.07	0.96 ± 0.07	0.94 ± 0.09
FOR$_{night}$	0.95 ± 0.09	0.96 ± 0.09	0.93 ± 0.1	0.96 ± 0.07	0.96 ± 0.07	0.93 ± 0.07
TAD	0.64 ± 0.1	0.74 ± 0.08	0.63 ± 0.09	0.69 ± 0.13	0.64 ± 0.2	0.57 ± 0.08

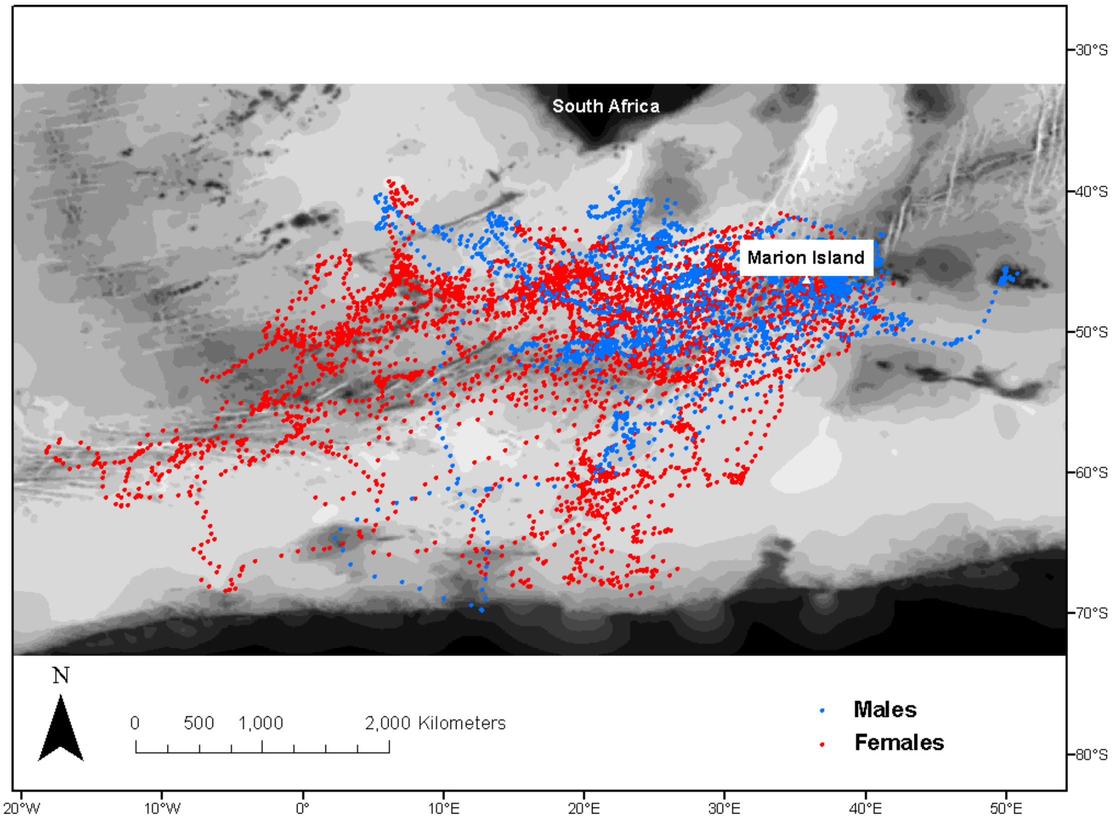

Figure 6.1: Map indicating daily averaged dive locations for the elephant seal tracks used in this study.

Most of the animals in our sample travelled in westerly and south-westerly directions away from Marion Island during their foraging migrations (Fig. 6.1). One subadult male travelled in an easterly direction however toward Îles Crozet. More detailed analyses of dive behaviours recorded by southern elephant seals in this sample are reported elsewhere (chapters 3 and 4).

Full models for dive parameters included age class (restricted to models for male dive parameters), FZ, migration, DVS, bottom depth, $T_{max}100$ and $T_{max}100.depth$ as fixed effects. Individual was included as random effect in all models. Autoregressive moving average autocorrelation functions were incorporated in all models with best fits to account for the inherent temporal autocorrelation evident in the data (Pinheiro & Bates 2004) (Table 6.3).

Table 6.3: Summary of models with best fits. ΔAIC_c = the difference in AIC_c between the final model and the initial full model, containing all parameters; RE = random effect. Correlation structures for all final models were autoregressive moving average (ARMA) functions.

Parameter	**Model**	**Δ AIC**	**Correlation structure**	**RE**
MALES				
$DDEP_{day}$	$\log(DDEP_{day})$ ~ AGE.CLASS + BOTTOM + DVS + FZ + Tmax100	715.21	ARMA (p = 2, q = 2)	44.17
$DDEP_{night}$	$\log(DDEP_{night})$ ~ AGE.CLASS + BOTTOM + DVS + Tmax100 + Tmax100.depth	623.03	ARMA (p = 2, q = 2)	11.8
$DDUR_{day}$	$DDUR_{day}$ ~ TDAY + AGE.CLASS + DVS + Tmax100	1 055.58	ARMA (p = 3, q = 3)	16.72
$DDUR_{night}$	$DDUR_{night}$ ~ TDAY + AGE.CLASS + MIGRATION + DVS	1 172.69	ARMA (p = 2, q = 2)	37.87
TAD	TAD ~ MIGRATION + DVS + Tmax100	332.59	ARMA (p = 2, q = 2)	20.73
FEMALES				
$DDEP_{day}$	$DDEP_{day}$ ~ TDAY + BOTTOM + DVS + FZ + Tmax100	1 195.32	ARMA (p = 2, q = 2)	< 0.01
$DDEP_{night}$	$DDEP_{night}$ ~ TDAY + BOTTOM + DVS + FZ + Tmax100 + Tmax100.depth	1 366.57	ARMA (p = 3, q = 3)	4.37
$DDUR_{day}$	$DDUR_{day}$ ~ TDAY + MIGRATION + DVS + Tmax100	2 579.27	ARMA (p = 1, q = 1)	< 0.01
$DDUR_{night}$	$DDUR_{night}$ ~ TDAY + DVS + Tmax100	2 394.83	ARMA (p = 2, q = 2)	< 0.01
TAD	TAD ~ DVS + Tmax100	490.26	ARMA (p = 2, q = 2)	< 0.01

Dive depths

Model results indicated that dive depths recorded during both day- and night-time for both sexes were significantly influenced by DVS (Tables 6.3 and 6.4). Dive depths recorded during day- and night-times by both males and females were also significantly influenced by T_{max}100 (Tables 6.3 and 6.4). A positive relationship was evident in all cases, with dives being deeper in warmer water temperatures (for example Fig. 6.2). Model coefficients indicated that this relationship was stronger for females (daytime = 9.24; night-time = 10.14) than for males (daytime = 0.03; night-time = 0.03). Mean night-time dive depths undertaken by both sexes were also significantly influenced by T_{max}100.depth, dives becoming shallower when the T_{max}100.depth is deeper (though maximum night-time dive depths were deeper than T_{max}100.depth in 96% of the dives recorded).

Female day-and night-time dive depths were further significantly influenced by TDAY and bottom depth. Both these variables exhibited a positive relationship with dive depth, with recorded dives being deeper in areas with deeper bathymetry (higher bottom depth values), and also becoming deeper as tracks become longer. Male night-time dive depths were also significantly influenced by bottom depth, though model coefficients indicated this influence to be small (< 0.00). Male daytime dive depths were additionally influenced by migration stage, with deeper dives recorded during PM migrations (687.6 ± 194.8 m) than during PB migrations (473.1 ± 101.5 m).

The random effects (track) explained between 0 and 4.4% of the variance in female dive depths, but between 11.8 and 44.2% of the variance in male dive depths (Table 6.3).

Table 6.4a: *F* test results indicating significant fixed effects on final models for male data. Boldface indicates statistically significant effects ($p \leq 0.05$). Parameter abbreviations are as for Table 6.1.

Parameter	Fixed effect	Coefficient	F	df	p
MALES					
DDEP$_{day}$	**Intercept**	**6.168**	**12489.83**	**1,1946**	**<.0001**
	AGE.CLASS	**-0.137**	**6.41**	**1,1946**	**0.011**
	BOTTOM	0.000	3.07	1,1946	0.080
	DVS	**0.123**	**593.25**	**1,1946**	**<.0001**
	FZ	0.032	0.87	1,1946	0.350
	Tmax100	**0.032**	**55.72**	**1,1946**	**<.0001**
DDEP$_{night}$	**(Intercept)**	**6.046**	**11846.10**	**1,1946**	**<.0001**
	AGE.CLASS	-0.093	1.63	1,1946	0.202
	BOTTOM	**0.000**	**28.97**	**1,1946**	**<.0001**
	DVS	**-0.151**	**475.51**	**1,1946**	**<.0001**
	Tmax100	**0.034**	**29.87**	**1,1946**	**<.0001**
	Tmax100.depth	**0.000**	**19.95**	**1,1946**	**<.0001**
DDUR$_{day}$	**(Intercept)**	**1787.539**	**432.06**	**1,1947**	**<.0001**
	TDAY	**2.208**	**18.12**	**1,1947**	**<.0001**
	AGE.CLASS	-271.850	4.43	1,1947	0.036
	DVS	**138.965**	**152.73**	**1,1947**	**<.0001**
	Tmax100	**36.831**	**17.55**	**1,1947**	**<.0001**
DDUR$_{night}$	**(Intercept)**	**2434.502**	**201.00**	**1,1947**	**<.0001**
	TDAY	**1.396**	**7.16**	**1,1947**	**0.008**
	AGE.CLASS	**-399.761**	**7.29**	**1,1947**	**0.007**
	MIGRATION	**-383.737**	**6.22**	**1,1947**	**0.013**
	DVS	**-96.071**	**127.96**	**1,1947**	**<.0001**
TAD	**(Intercept)**	**0.736**	**1656.53**	**1,1580**	**<.0001**
	MIGRATION	**-0.113**	**19.65**	**1,1580**	**<.0001**
	DVS	**0.006**	**6.28**	**1,1580**	**0.012**
	Tmax100	**-0.003**	**4.35**	**1,1580**	**0.037**

Table 6.4b: *F* test results indicating significant fixed effects on final models for female data. Boldface indicates statistically significant effects ($p \leq 0.05$). Parameter abbreviations are as for Table 6.1.

Parameter	Fixed effect	Coefficient	F	df	p
FEMALES					
$\mathrm{DDEP}_{\mathrm{day}}$	**(Intercept)**	**302.608**	**6171.13**	**1,3286**	**<.0001**
	TDAY	**0.470**	**54.24**	**1,3286**	**<.0001**
	BOTTOM	**0.012**	**46.27**	**1,3286**	**<.0001**
	DVS	**75.880**	**1329.41**	**1,3286**	**<.0001**
	FZ	7.956	0.71	1,3286	0.401
	Tmax100	**9.241**	**40.74**	**1,3286**	**<.0001**
$\mathrm{DDEP}_{\mathrm{night}}$	**(Intercept)**	**342.065**	**2090.03**	**1,3285**	**<.0001**
	TDAY	**0.127**	**5.76**	**1,3285**	**0.016**
	BOTTOM	**0.008**	**9.78**	**1,3285**	**0.002**
	DVS	**-35.552**	**386.32**	**1,3285**	**<.0001**
	FZ	5.201	1.40	1,3285	0.236
	Tmax100	**10.142**	**42.93**	**1,3285**	**<.0001**
	Tmax100.depth	**0.066**	**18.80**	**1,3285**	**<.0001**
$\mathrm{DDUR}_{\mathrm{day}}$	**(Intercept)**	**1399.331**	**747.68**	**1,3287**	**<.0001**
	rank	**3.332**	**74.37**	**1,3287**	**<.0001**
	MIGRATION	-142.708	2.75	1,3287	0.097
	DVS	**160.478**	**341.45**	**1,3287**	**<.0001**
	Tmax100	**12.975**	**4.73**	**1,3287**	**0.030**
$\mathrm{DDUR}_{\mathrm{night}}$	**(Intercept)**	**1384.860**	**1055.44**	**1,3288**	**<.0001**
	TDAY	**2.727**	**79.05**	**1,3288**	**<.0001**
	DVS	**-61.133**	**90.93**	**1,3288**	**<.0001**
	Tmax100	**-24.698**	**27.52**	**1,3288**	**<.0001**
TAD	**(Intercept)**	**0.702**	**2641.65**	**1,2091**	**<.0001**
	DVS	**0.011**	**7.50**	**1,2091**	**0.006**
	Tmax100	**-0.010**	**27.87**	**1,2091**	**<.0001**

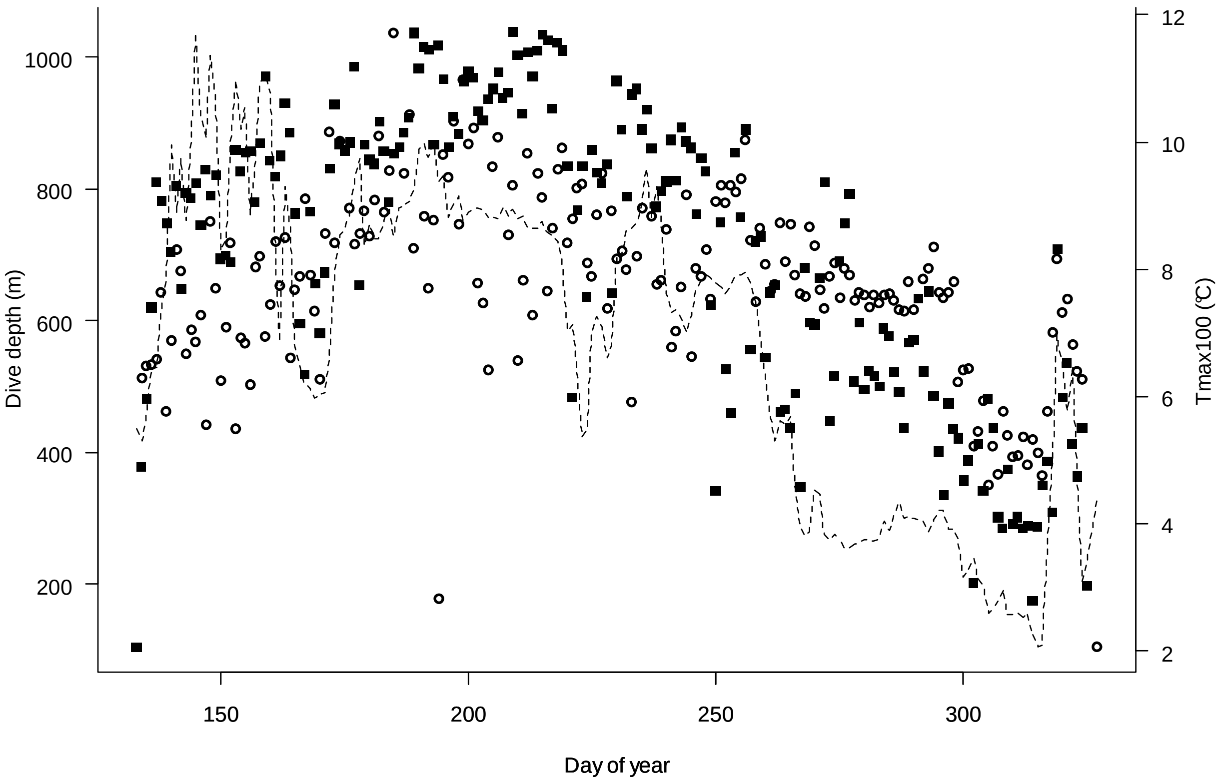

Figure 6.2: Example plot indicating the relationship in mean daily dive depths (open circles = daytime; filled block = night-time) and $T_{max}100$ (dotted line) recorded for individual OO405.

Dive durations

Excluding night-time dives undertaken by male seals, dive durations were significantly influenced by $T_{max}100$ (Table 6.3 and 6.4). This relationship was positive for all daytime dives, resulting in longer dives being undertaken when $T_{max}100$ increased. However, a negative relationship was evident for night-time dives undertaken by seals and dives were shorter when $T_{max}100$ increased. Model coefficients indicated that these relationships were slightly stronger for males, than for females (Table 6.4).

Male night-time dive durations were further influenced by migration stage and age class. PM dives (27.5 ± 9 min) were longer than PB dives (24.4 ± 5 min), and dives performed by adult males were longer on average than subadult males (adults: 28.4 ± 7.7 min; subadults: 26.7 ± 9 min). Female night-time dive durations also differed between migration stages (PM:

25.3 ± 7.1 min; PB: 16.3 ± 3 min). While migration stage was included in the most parsimonious model for female night-time dive durations, *F* test results indicated this effect not to be statistically significant (Table 6.4).

Dive durations recorded for day- and night-time dives by both sexes were significantly influenced by DVS and TDAY (Table 6.3 and 6.4). Dive durations displayed a positive relationship with TDAY, becoming longer as TDAY increased. DVS influenced dive durations in a similar manner to dive depths. Daytime dive durations were longer when animals displayed positive DVS (males: 36.5 ± 10.1 min; females: 33.6 ± 9.4 min) than when they displayed neutral (males: 34.8 ± 12 min; females: 32 ± 10.9 min) or negative (males: 35.2 ± 12 min; females: 28.5 ± 11.8 min) DVS. Night-time dive durations were longer when animals displayed negative DVS (males: 32.8 ± 9.1 min; females: 27.1 ± 8.6 min) when compared to night-time dives while animals displayed neutral (males: 26.7 ± 8.4 min; females: 24.8 ± 7.6 min) or positive (males: 25.6 ± 8 min; females: 23.7 ± 7.1 min) DVS.

The random effects (track) explained less than 0.01% of the variance in female dive durations, and between 16.7% and 37.9% of the variance in male dive durations (Table 6.3).

TAD

All TAD values were significantly influenced by $T_{max}100$ (Tables 6.3 and 6.4). TAD values approached values of approximately 0.5, as $T_{max}100$ values increased, while cooler $T_{max}100$ values were associated with TAD values closer to 1 (for example Fig. 6.3). This relationship was stronger in dives recorded for females (Coefficient = -0.01) than for males (Coefficient = -0.003). Male TAD values were further influenced by migration stage, where TAD values tended to be higher during PB migrations (0.74 ± 0.08), when compared to PM migrations (0.63 ± 0.1). Female TAD values were also influenced by DVS and tended to be slightly higher when animals displayed a positive DVS (0.68 ± 0.1) when compared to neutral (0.66 ± 0.11) and negative strategies (0.66 ± 0.12). Male TAD values were also influenced by DVS, though TAD values were similar between DVS strategies (Positive DVS: 0.64 ± 0.1; Neutral DVS: 0.64 ± 0.12; Negative DVS: 0.65 ± 0.09).

The random effects (track) explained less than 0.01% of the variance in female TAD values, and 20.7% of the variance in male dive TAD values (Table 6.3).

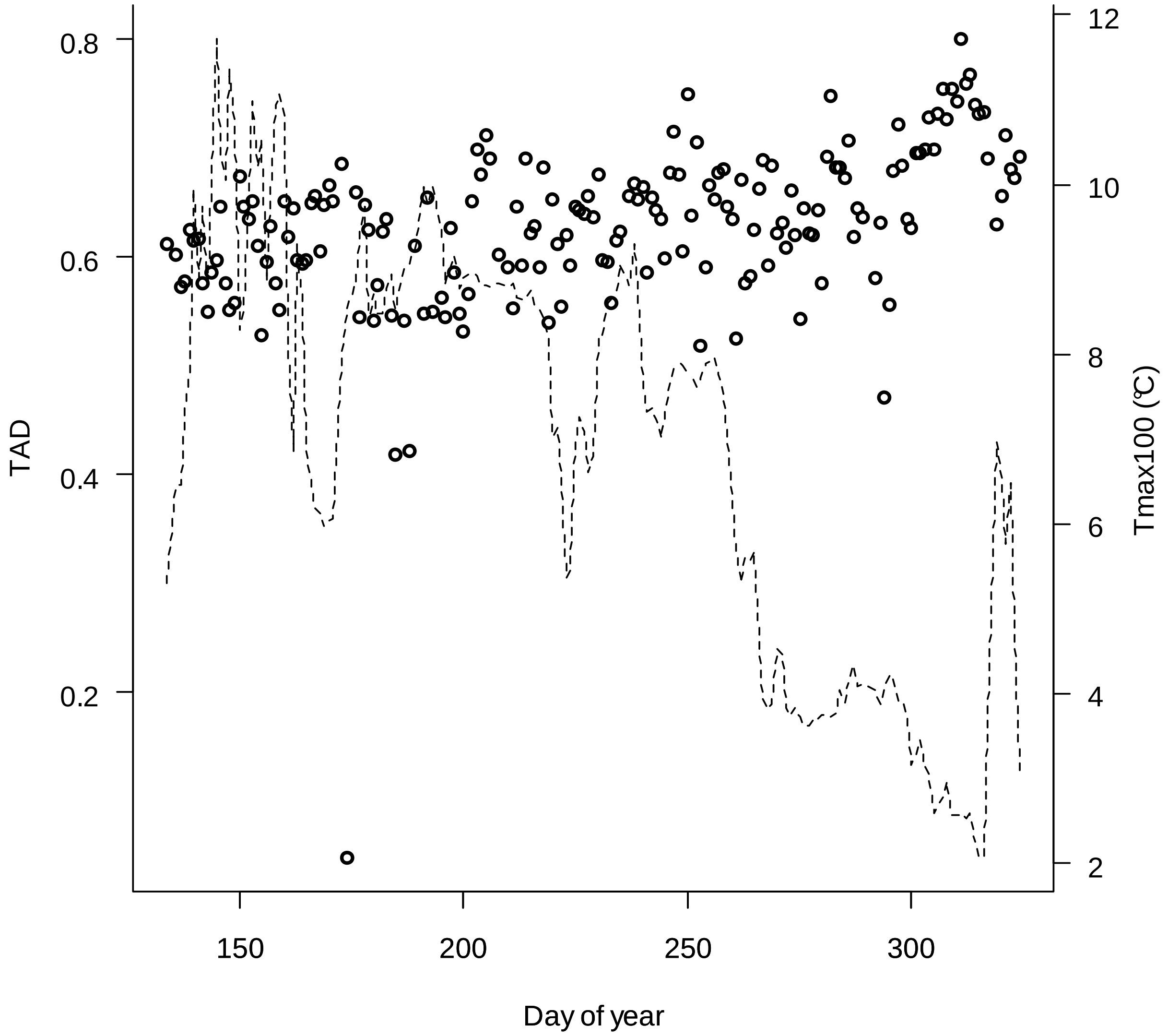

Figure 6.3: Example plot indicating the relationship between TAD (open circles) and $T_{max}100$ (dotted line) recorded for individual OO405.

Ratio of U- and W-shaped dives

The distributions of data relating to the ratio of U- and W-shaped dives were non-normal (also after various transformations) and did not allow for the modelling of this variable in relation to other parameters. However, plots of this ratio in relation to the TAD values of U- and W-shaped dives did not indicate any clear relationship between these parameters (Fig.

6.4). Most of the dives were classified as either U- or W-shaped (daytime: 95%; night-time: 94.3%) (Table 6.2) and no increases in occurrence of these dive types were evidently associated with specific TAD values.

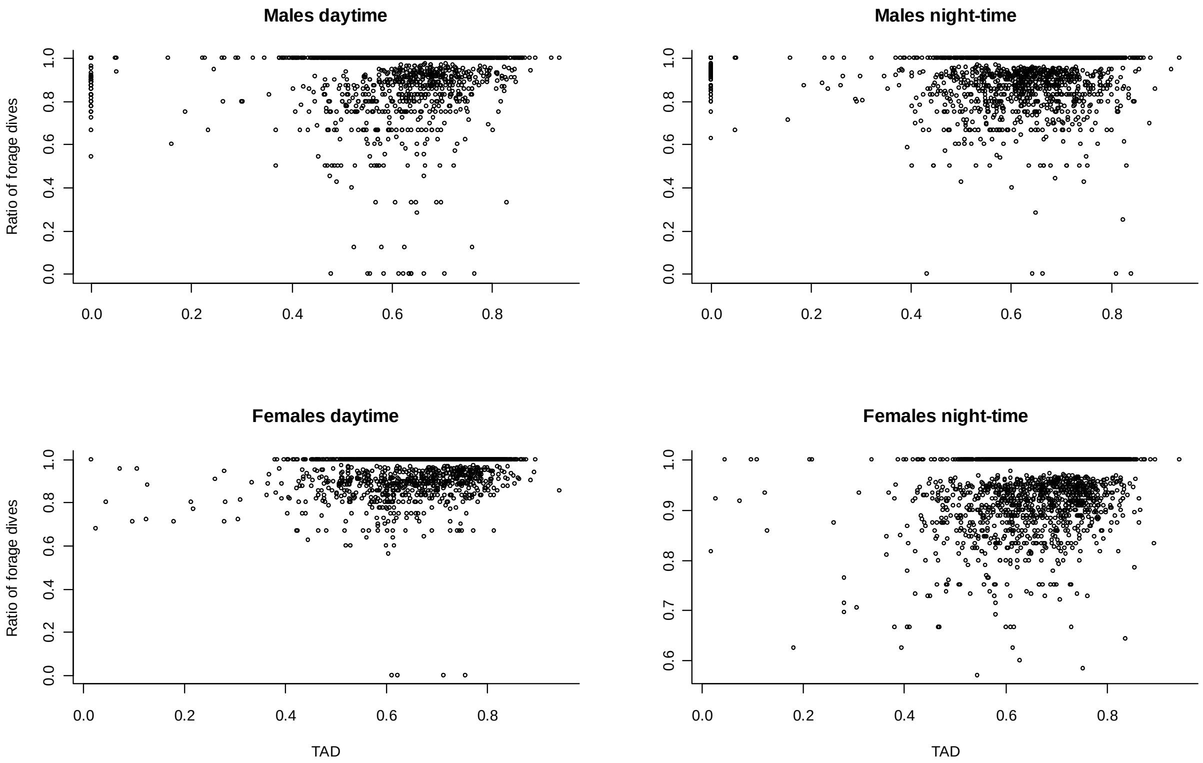

Figure 6.4: Scatterplots of mean daily TAD values and the ratio of U- and W-shaped dives recorded in our sample.

Discussion

The diving behaviour of southern elephant seals from Marion Island is influenced by factors such as migration stage, track day, bathymetry, diel vertical strategy and temperature at depth. Variation in the dive behaviour of animals also exists between individuals and this plays an important role in explaining the models.

Influence of $T_{max}100$

Our results clearly illustrate a link between water temperatures at depths greater than 100m and the dive behaviour of Marion Island southern elephant seals. Best models indicated that $T_{max}100$ significantly influenced dive depths, dive durations (except male, night-time dive durations), as well as the relative portions of time animals spent at the targeted depths of dives (TAD). This relationship was stronger for female seals, compared to males (Table 6.3), suggesting that increases in water temperature result in females increasing their dive depths proportionally more than males. The positive relationship of daytime dive durations with $T_{max}100$ was expected, given that deeper dives are mostly associated with increases in dive duration (Bennet et al. 2001). However, a less clear relationship existed between night-time dive durations exhibited by females and $T_{max}100$, where animals appeared to dive for slightly shorter periods of time when $T_{max}100$ increased (though still to deeper depths). Further investigation into the potential role of displaying negative DVS may clarify this. Dive durations in southern elephant seal females tend to be positively related to body size (Hindell et al. 2000; Irvine et al. 2000; Hassrick et al. 2010). Unfortunately body size or condition data were unavailable for many of the seals in our sample and we were therefore unable to quantify the influence of differences in body size on their dive behaviour.

The depth at which $T_{max}100$ values were recorded ($T_{max}100$.depth) was less often related to dive parameters in our study. Night-time dive depths did exhibit a significant positive relationship with $T_{max}100$.depth, indicating that seals tended to dive deeper when the $T_{max}100$ water layer occurred at increased depths. The influence of $T_{max}100$.depth on dive depths was substantially less in all cases than the $T_{max}100$ values themselves. While there existed a statistically significant correlation between night-time dive depths and $T_{max}100$.depth, this relationship was so weak (-0.13 and -0.07 for males and females respectively) that it was not considered likely to influence the model outputs. While the Southern Ocean is characterised by thermal stratification in near surface waters, particularly in the Subantarctic (Pollard et al. 2002), comparatively weaker differences are observed at depth (Anilkumar et al. 2006). This may explain the general lack of influence of $T_{max}100$.depth in our models. It further suggests that Marion Island elephant seals appear not to target vertical discontinuities in the thermal properties of water masses, as observed for one seal from South Georgia (Boyd & Arnbom

1991). Similar results to the present study have been reported for northern elephant seals (*M. angustirostris*) (Hakoyama et al. 1994).

Increased water temperatures at depth also influence dive type. Both male and female seals undertook dives with more equal distributions of time spent at the various depths encountered in areas with increased water temperature (dives approaching V-shapes). Since night-time dives tended to be deeper, but shorter in areas with warmer water, animals were able to spend more time at targeted dive depths in colder waters, resulting in dives tending to TAD values closer to 1 in areas with cooler water. We restricted the TAD models to dives that were identified as being U- or W-shaped dives, and likely to have a foraging purpose. Within this category of dives, the seals in our sample spent proportionally less time at depth in areas with increased water temperature, when compared to colder areas. We did not assess foraging success in this investigation, though a number of proxies for foraging success have been proposed (see for example Robinson et al. (2010) and the references therein). However, the reduction in time spent at depth when animals were encountering warmer water masses, suggests a smaller likelihood of successful foraging in such environments.

It is possible that elephant seals may compensate for being less able to spend time at targeted depths (while performing forage-type dives) by either increasing the absolute number of dives undertaken or by increasing the ratio of forage-type dives in relation to other dive types. Since satellite-uplink rates were variable throughout migrations we did not have information available regarding the absolute number of dives performed by individuals during specific portions of tracks. The nature of the data relating to the relative proportions of various dive types exhibited further did not allow for the modelling of dive-type ratios in relation to TAD of forage-type dives. However, plots of this data in relation to TAD seem to indicate no pattern of compensating for less time at targeted depths by increases in forage-type dives. Our analyses could not exclude such a strategy within a statistical framework and more investigations using archival data recorders may clarify this further.

The effect of temperature on elephant seal dive behaviour is likely due to the influence of temperature on the distribution of prey species. The Southern Ocean is warming (Gille 2002), and climate models predict that this warming is likely to continue (Solomon et al. 2009;

Trathan & Agnew 2010). However, an acute limitation on studies of the Southern Ocean is its severe inaccessibility, especially during austral winter, resulting in the reliance on long-term climatic model data, rather than shipboard observations. The design of ARGO was to provide greatly improved spatial and temporal sampling in remote and harsh regions where observations have been severely hampered. Recently, using combined ARGO and XBT data, an increase in the upper layer (top 700 m) heat anomaly of 0.64W m^{-2} over the past 16 years was demonstrated (Lyman et al. 2010). At the PEI this warming trend is certainly evident in daily sea surface temperature readings which increased by 1.4°C over a 50 year period (Mélice et al. 2003). Furthermore, ARGO data for the period 2004-2010 also indicated an increase of 0.15°C in the Subantarctic zone in the top 600 m (Fig. 6.5). Although this record is only for the past 8 years it does compare well to model data, which shows a significant southward shift in the subsurface expression ($z = 400$ m) of the SAF (Allen et al. submitted). A recent investigation into the multi-decadal warming of water masses exported north of the ACC, namely Antarctic Intermediate Water (AAIW) (Schmidtko & Johnson in press) has shown that the strongest warming trend in the upper 1 000 m is found directly north of the Subantarctic Front (Gille 2002), and compares well with the warming trend observed in Fig. 6.5.

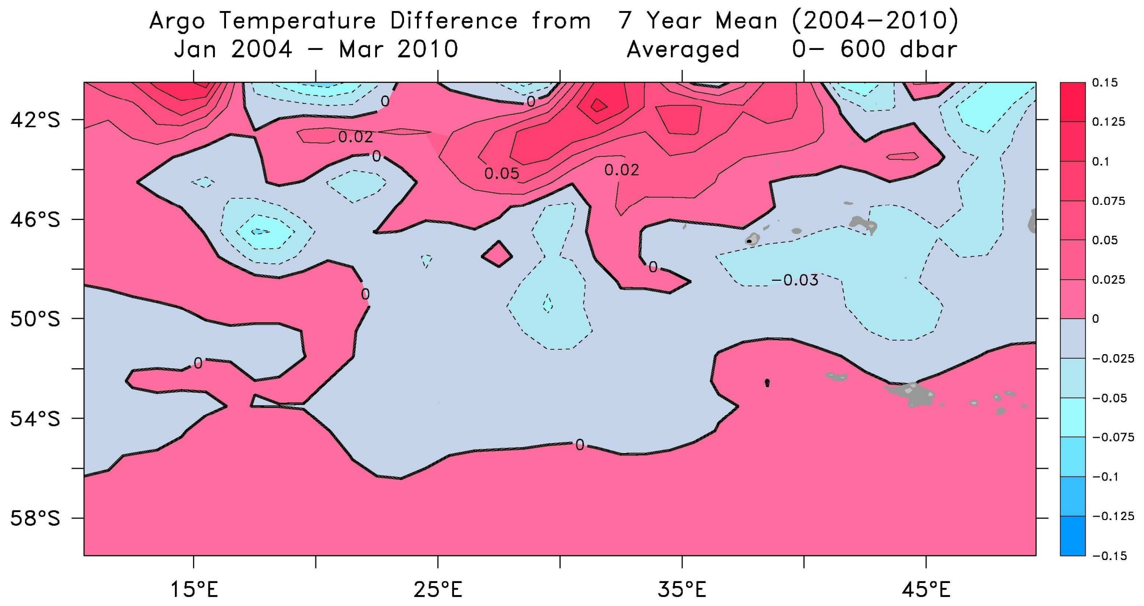

Figure 5: ARGO profiling data highlighting the difference in temperature from the mean for the period 2004-2010 for the upper 600 m. Warming trends correlate with the northern and southern boundaries of the ACC, and in particular north of the Prince Edward Islands along/and north of the SAF.

One impact of this warming has been a change within the species composition of the zooplankton. A recent review (Pakhomov & Chown 2003) of their composition around the PEI suggests that the contribution of Antarctic species decreased by approximately 20% since the 1980s. In contrast, subtropical species (indicative of warmer water masses) have increased from 6% to 26%. This finding is further supported by accidental catches of subtropical fish species in the PFZ during long-line fishing. Thus, it is clear that warming will lead to changes in the distribution of fish stocks, and a likely general poleward shift in fish distributions, accompanied by fish occurring at deeper depths (Perry et al. 2005; Dulvy et al. 2008; Nye et al. 2009). While the diet of southern elephant seals at Marion Island is poorly known, results from other investigations indicate that southern elephant seals largely predate on myctophid fish and squid (Slip 1995; Lewis et al. 2006; Cherel et al. 2008; Bailleul et al. 2010a). An increase in temperature in the top 1 000 m will certainly influence the foraging behaviour of the Prince Edward Island’s top predators, which could respond by either shifting their foraging grounds polewards or adapting their dive behaviour. Since southern elephant seals exhibit plasticity in forage strategies, it has been suggested that they may be able to adapt relatively easily to environmental changes (Biuw et al. 2010). However, the southern elephant seals of Marion Island represent one of the most northern breeding colonies of this species and are, together with animals from neighbouring Prince Edward Island, comparatively isolated (closest landfall being Crozet islands ~ 1 000 km east). While they are wide-ranging animals, sometimes travelling as far south as the Antarctic continental shelf, this behaviour is not common and most animals forage primarily pelagically in inter-frontal zones (this study, Jonker & Bester 1998; Tosh 2010). The location of their terrestrial breeding habitat potentially limits their ability to undertake range shifts, thus necessitating the seals to adapt their dive behaviour. Elephant seals from Marion Island are known to be extreme divers, generally diving deeper than has been recorded for other populations (chapters 3 and 4). Shifts in the vertical distribution of prey species due to changes in water temperature may therefore lead to seals having to dive even deeper (requiring longer dive durations), resulting in greater physiological costs associated with diving. This effect may be greater in female southern elephant seals than males. While we did not record behaviour from juvenile animals in our sample, it is expected that such influences may be even greater on juveniles due to their reduced diving capabilities (Field et al. 2005b).

Influence of diel vertical strategy

The seals in our sample exhibited a range of diel diving strategies, ranging from positive (deeper dive depths during the day, when compared to night-time dives) to negative (deeper dive depths during the night, when compared to daytime dives) strategies. While the positive DVS is common amongst elephant seals that forage in pelagic environments (Hindell 1991; Jonker & Bester 1994), the negative strategy is less common and has only recently been described for seals from Marion Island (Jonker 1997; chapter 3 (this study)). DVS predictably influenced both the depth and durations of dives made by seals in our sample. Seals further tended to spend more time at depth (with calculated TAD values closer to 1) when exhibiting a positive DVS. The differences in TAD values obtained for elephant seals exhibiting different diel strategies indicate that elephant seals are able to spend more time at targeted depths, when exhibiting positive strategies, compared to neutral- or negative strategies. Since little dietary information is available for this population of southern elephant seals, interpreting the differences in DVS is difficult. Undertaking dives with lower TAD values that approach 0.5 (i.e. displaying a time-depth profile that approaches a V-shape) is normally considered to represent exploration-type dives that likely carry substantial physiological costs (given that little to no foraging takes place). Explaining why an increase of such dive behaviour is associated with the neutral- or negative DVS will require more information related to prey species taken (and quantity) whilst displaying such different strategies.

Influence of migration stage

Differences in dive behaviour between migration stages were evident in night-time dive durations and time at depth (TAD) values attained by male southern elephant seals. Males made longer night-time dives during PM trips when compared to PB trips. Males tracked on PB migrations were older than males tracked on PM migrations (PB = 9.4 ± 1.6 yr; PM = 5.4 ± 2.5 yr), suggesting that males on PB migrations in our sample were likely to be larger than males tracked on PM migrations. Since PM males dived for longer than PB males, irrespective of body size, the shallower dives observed during PB migrations may be due to a loss of body condition and fitness resulting from participating in the breeding haulout (Carlini et al. 2004; Galimberti et al. 2007). Furthermore, dive durations increase as migrations progress (Bennet et al. 2001), and since the PB migrations are shorter than the PM migrations, animals have less time available to them in the PB migrations to improve their fitness enough to sustain longer dive durations. An alternative explanation may be that food resources are more readily available in the austral summer, not requiring such long dives. Also, variations in day length between migration stages were likely to influence the diel patterns of vertically migrating prey, influencing the observed dive behaviours. We did not account for variations in day length here. Adult males seals also spent more time at depth during PB migrations (higher TAD values), compared to PM migrations. Shallower dives during PB migrations may allow the seals greater amounts of time at targeted depths, accessing readily available food resources and thereby resulting in more dives with TAD values closer to 1.

Female elephant seals in our sample also exhibited differences in dive duration between migrations, though the influence of migration stage was not identified as a significant influence in the most parsimonious model. Dive durations are known to be influenced by body size and condition (Irvine et al. 2000; Hassrick et al. 2010). It is therefore likely that the differences observed in dive durations are due to differences in condition upon departing for

PM vs. PB migrations. Our results could however not exclude the possibility of differences in forage strategy and/or diet, or the influence of day length variation, between the migration stages affecting the dive durations of Marion Island elephant seals.

Influence of Track day

Track day had a significant influence on various dive parameters modelled here, including all models for dive durations, and dive depths of female southern elephant seals. Dive durations tend to increase as a function of time during migrations, and could be as a result of increases in muscle oxygen storage ability and fitness (Bennet et al. 2001). Track day influences on the dive depths of female southern elephant seals may be related to the influences of track day on dive durations of this group. This may indicate that dive depths are further constrained by physiological ability of female elephant seals.

Conclusion

Elephant seals routinely dive beyond their calculated aerobic dive limits (Butler 2006) and are capable of tolerating extreme hypoxemia (Meir et al. 2009). Our results suggest that southern elephant seals from Marion Island tend to dive deeper and spend less time at targeted depths in warmer water bodies. This is likely the result of vertical shifts in the distribution of preferred prey in relation to water temperature. Under current climate predictions, the world's oceans will continue warming and prey distributional shifts due to ocean warming will likely lead to the Marion Island elephant seals having to either shift their migration ranges poleward, or target deeper water layers. Shifts in migration ranges (particularly the shorter PB migrations) may be constrained by the comparatively low latitude of the PEI, necessitating deeper diving strategies. Since the Marion Island elephant seals are possibly diving close to their physiological limits under current conditions, such deeper diving may lead to greater long-term physiological costs and decreased survivorship in this population. Investigations to determine the preferred prey species of southern elephant seals (and their respective habitat preferences and thermal tolerances) are required to better quantify the potential impacts of climate changes on the foraging behaviour of this top predator.

CHAPTER SEVEN: GENERAL CONCLUSION

Southern elephant seals are major consumers and top predators in the Southern Ocean (Guinet et al. 1996; Hindell et al. 2003). Much is known about their behaviour on land, population status and increasingly about their movements at sea (Le Boeuf & Laws 1994b). The elephant seal population at Marion Island is unique from the world population for a number of reasons. Firstly, the location of Marion Island, its distance from continental shelves and the Antarctic ice edge results in animals having to utilise different environments from other major populations, or travel greater distances to similar habitats. The ongoing long-term mark-resighting investigation on elephant seals at Marion Island (Bester 1988b) provides researchers with a unique dataset providing the histories of individual animals, with information that includes their haulout histories on the island, age, birth sites and reproductive success and/or status. The at-sea movements and limited dive behaviour of Marion Island elephant seals were previously assessed mainly using geolocation instruments and time-depth recorders (Bester 1989; Bester & Pansegrouw 1992; Jonker & Bester 1994; 1998). In recent years satellite-linked devices have increasingly been deployed on Marion Island elephant seals providing more accurate at-sea movement accounts and in some instances dive records for entire tracks (Tosh 2010). This thesis aimed to describe the underwater habitat use of southern elephant seals from Marion Island and to place such behaviour into an ecological and evolutionary context.

The results I obtained from analysing dive data obtained via satellite-relay data loggers (SRDLs, Sea Mammal Research Institute, University of St. Andrews, Scotland) provided new insights into the water column use of Marion Island elephant seals in a number of ways. By combining data from such deployments with information obtained through the long-term mark-resighting programme I was firstly able to quantify the lifetime habitat use of southern elephant seals (Chapter 2). The results from this investigation indicated that elephant seals from Marion Island appear to perform deeper dives more regularly than animals from other elephant seal populations, possibly resulting in greater physiological stresses. The extreme lifestyles quantified through this investigation (with animals spending approximately 77% of their lives at sea, and large percentages of this at depths deeper than 100 m, and often at depths deeper than 700 m), combined with the comparatively short reproductive lifespans of

Marion Island animals (at least compared to animals from Macquarie Island), led to a "deeper diving – shorter life" hypothesis. Accordingly, I propose that the extreme dive behaviour of Marion Island elephant seals may incur additional physiological costs that are not as extreme in other shallower-diving populations. This hypothesis will require further investigation combining more detailed information from other southern elephant seal populations, and the continued monitoring of the at-sea behaviour of elephant seals in relation to their reproductive success and longevities.

I next provided more detailed descriptions of the water column usage of female (Chapter 3) and male (Chapter 4) elephant seals from Marion Island. For these descriptions I developed a new measure of forage effort, using a daily averaged ratio of dives where animals displayed greater-than-average amounts of time during the bottom phases of U-shaped dives, compared to dives with less-than-average bottom times. Animals mostly foraged pelagically, where they employed diverse strategies that resulted in positive, negative and neutral vertical diel variations in dive depths. Females displayed higher forage effort in areas further away from Marion Island, though opportunistic foraging evidently also took place in close proximity to the island during their travelling phases. Male animals displayed more variation in forage strategies, though they too mostly employed pelagic foraging strategies, rarely diving to the seafloor. A few individuals did however dive to the seafloor occasionally, particularly over the shelf area between Marion Island and Prince Edward Island, as well as over the Agulhas Rise. Adult males mostly focussed their forage effort in closer proximity to the island, compared to subadult males. The purpose of deploying a negative diel vertical strategy remains unknown and further investigations aimed at identifying prey types associated with different dive strategies are required.

The driving factors behind the evident sexual segregation in dive behaviour of southern elephant seals were investigated in Chapter 5. Here I employed mixed-effects models to elucidate the influence of size (body length), sex and age on the dive depths and dive durations of animals that utilised similar areas within the Southern Ocean. Mixed-effects models allow for the explicit modelling of temporal autocorrelation inherent to most telemetry studies, as well as allowing for different variances between random effects (individual animals in this case). While individual variation explained much of the resulting models, clear trends emerged regarding the influences of sex and size on the dive behaviour of animals. Sex consistently influenced the dive depths of elephant seals, while size did not appear to substantially influence this variable. Dive durations were, however, clearly influenced by the size of animals and sex did not play a significant role here. These results support previous investigations that implied physiological capability to be the driving factor behind how long dives can be (Hindell et al. 2000; Irvine et al. 2000). The role of sex, irrespective of size, in dive depths indicates that differences exist between sexes in forage selection and support hypotheses for resource partitioning between sexes and the possible avoidance of intra-specific competition in this species (Field et al. 2007a).

I again employed mixed-effects models to investigate the influences of *in situ* temperature at depth, the depths at which the T_{max} value occurs in the water column, water depth and various demographic and behavioural variables on the dive depths, dive durations and time-at-depth index (TAD) (as put forward by Fedak et al. 2001) values of individual dives (Chapter 6). Individual variation explained large proportions of the variation in dive variables and dive variables appeared to be influenced by a number of factors. Dive depths and TAD values were, however, consistently influenced by temperature at depth. These relationships suggested that seals tended to dive to greater depths when foraging in areas characterised by warmer water. The time animals were able to spend at preferred depths was shorter in such areas, indicating that elephant seals were presumably less successful at foraging in such warmer water masses. The relationship between the dive parameters measured and *in situ* temperature is likely an indirect one and related to potential prey species preferring cooler water temperatures (present at greater depths in the warmer water masses). Current climate predictions suggest continued warming of the Southern Ocean, likely resulting in a poleward shift and a concurrent deepening of suitable habitat of potential prey species for elephant seals (Perry et al. 2005; Dulvy et al. 2008; Nye et al. 2009; Trathan & Agnew 2010). Such shifts in prey distributions would likely result in elephant seals having to either dive to even more extreme depths for foraging and/or travel greater distances poleward. While elephant seals in general are considered likely to be able to adapt to predicted climate changes in the Southern Ocean due to their evident behavioural plasticity (Biuw et al. 2010), the Marion Island population may be less likely to successfully adapt given their current extreme diving habits (chapter 2). More detailed investigations into the exact prey species of

Marion Island's southern elephant seals (and their distributions and well as thermal preferences) are required to better quantify the potential influences of projected climate changes on these predators.

This research provided a detailed account of the water column use of Marion Island southern elephant seals and explored the evolutionary influences of sexual segregation and ecological influences of surrounding environments on their dive behaviour. Results from this investigation suggested that substantial inter-population differences in forage strategy and water column use may be present in this species, providing impetus for future comparative work to elucidate such differences. Current limitations to further interpretation of this information are mainly due to a lack of species-specific information of the diet of southern elephant seals, and the distributions of such prey species. The relative course-scale information provided by SRDLs of the dive behaviour of elephant seals provides good insights into the general water column use of elephant seals in time and space. However, detailed measures of actual foraging and forage success are still lacking. Advances in accelerometer- and camera systems suitable for deployment on southern elephant seals hold much promise to help answer some of these questions.

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APPENDIX A: SUPPLEMENTARY MATERIAL FOR CHAPTER 2

Methods

Depth bin calculations

For each transmitted dive profile we therefore calculated the following:

Interpolated depth points between transmitted depth points (X_n, n = 0.25 - 4.75 – see Figure S1) based on the following:

$$X_n = D_n + y(D_{n+1} - D_n)$$

where X = interpolated depth point

D = transmitted depth point preceding the interpolated depth point being estimated

y = fraction of interpolated depth point (e.g. if the position of X = 1.25 (first interpolated depth point between transmitted depths 1 and 2), then y = 0.25).

Percentages of time passed at each interpolated depth point (Q_n, n = 0.25 - 4.75), assuming constant swim speeds:

$$Q_n = T_n + y(T_{n+1} - T_n)$$

where Q = interpolated percentage time value

T = transmitted percentage time value for depth point preceding interpolated depth point.

Actual time values between successive depth points (transmitted and interpolated) (A_n, n = 0 – 21):

$$A_n = \left(\frac{Dive\_duration}{100} \right) \times (X_n - X_{n-1})$$

Table A1: Summary of dive data obtained from southern elephant seals from Marion Island. Type of migration are indicated such that PM = post-moult migration and PB = post-breeding migration.

					Overall activity (%)		**Maximum depths (m)**			**Dive durations (min)**			**Surface durations (min)**		**At sea activity (%)**	
Animal (track number)	**Sex**	**Age-class**	**Age**	**Migration**	**At sea**	**On land**	**Mean**	**Max.**	**SD**	**Mean**	**Max.**	**SD**	**Mean**	**SD**	**Diving**	**At surface**
BB081 (1)	m	subadult	5	PM	86.3	13.8	599.1	1 678	241.1	32.58	95.25	12.78	2.36	0.71	93.3	6.7
BB116 (1)	m	subadult	4	PM	86.9	13.1	487.2	1 229	226.8	30.57	95.25	8.36	1.97	1.13	94.0	6.0
BB128 (1)	m	subadult	5	PM	85.4	14.6	578.6	1 646	224.9	31.87	95.25	12.91	2.56	0.77	92.6	7.4
BB151 (1)	m	subadult	2	PM	77.3	22.7	542.8	1 262	187.2	30.83	88.25	11.75	2.33	0.71	93.0	7.0
BB191 (1)	f	adult	5	PM	87.9	12.1	458.8	1 006	154.2	23.75	84.25	8.86	2.27	1.04	91.3	8.7
BB253 (1)	m	subadult	2	PM	76.2	23.8	507.3	1 262	186.1	21.27	88.25	6.82	1.97	0.65	91.5	8.5
BB263 (1)	m	subadult	3	PM	86.5	13.5	601.1	1 550	214.4	26.02	77.25	9.00	2.22	0.61	92.1	7.9
GG178 (1)	m	adult	7	PM	77.1	22.9	543.5	1 129	184.5	31.60	73.25	6.50	2.82	1.13	91.8	8.2
GG335 (1)	f	adult	7	PM	91.2	8.8	454.8	1 166	211.2	33.17	95.25	20.73	2.24	1.01	93.7	6.3
GG335 (2)	f	adult	8	PB	91.2	8.8	296.6	974	202.4	17.28	95.25	15.59	2.80	1.24	86.0	14.0
GG335 (3)	f	adult	8	PM	91.2	8.8	493	1 230	192.6	32.12	95.25	13.16	2.26	0.87	93.4	6.6
OO021 (1)	f	adult	5	PM	82.1	17.9	477.2	1 134	157.8	27.67	85.25	9.19	2.14	0.68	92.8	7.2
OO021 (2)	f	adult	6	PM	82.1	17.9	461.8	1 609	144.9	29.00	95.25	9.97	2.12	0.65	93.2	6.8
OO052 (1)	m	subadult	4	PM	82.3	17.7	624.4	1 678	275.8	35.92	80.25	11.70	2.21	0.61	94.2	5.8
OO052 (2)	m	subadult	5	PM	82.3	17.7	622.6	1 629	329	44.50	95.25	15.91	2.70	1.02	94.3	5.7
OO052 (3)	m	adult	6	PM	73.2	26.8	519.1	1 902	294.2	36.72	95.25	15.52	2.42	0.76	93.8	6.2
OO086 (1)	m	subadult	3	PM	89.9	10.1	573	1 550	242.1	27.35	95.25	11.80	2.09	0.84	92.9	7.1
OO371 (1)	f	adult	5	PM	88.1	11.9	481.9	1 262	154.4	29.98	87.25	10.59	2.26	0.70	93.0	7.0
OO405 (1)	m	subadult	2	PM	85.8	14.2	513.7	1 902	188.4	23.60	79.25	7.93	2.02	0.53	92.1	7.9
OO418 (1)	f	adult	6	PM	87.6	12.4	436.5	1 014	182.8	24.22	75.25	8.75	2.32	0.58	91.3	8.7
PO043 (1)	f	adult	8	PM	88.2	11.8	292.3	870	174.5	18.12	95.25	18.23	4.01	2.79	81.9	18.1

PO043 (2)	f	adult	9	PM	88.2	11.8	497.4	1 189	175.3	27.93	91.25	10.99	2.31	0.70	92.3	7.7
PO225 (1)	m	adult	8	PM	77.0	23.0	500.9	1 138	196.8	28.58	57.25	9.79	3.13	0.93	90.1	9.9
PO225 (2)	m	adult	10	PB	77.0	23.0	444.1	1 129	134.6	30.37	74.25	7.27	2.89	0.56	91.3	8.7
RG017 (1)	f	adult	10	PM	91.6	8.4	536.3	1 262	203.7	30.65	83.25	10.54	2.31	1.00	93.0	7.0
RR009 (1)	m	subadult	3	PB	79.5	20.5	308.5	942	173.4	15.77	95.25	16.72	1.65	0.97	90.5	9.5
RR483 (1)	f	adult	3	PB	86.2	13.8	413.8	943.8	149	17.92	40.25	5.86	2.19	0.77	89.1	10.9
WB057 (1)	m	adult	14	PM	81.4	18.6	1040	2 149	639.2	33.40	73.25	8.42	4.10	1.39	89.1	10.9
WR029 (1)	m	adult	11	PB	76.7	23.3	359.8	1 169	111.4	23.43	56.25	5.22	2.90	0.64	89.1	10.9
WW005 (1)	m	adult	7	PB	76.7	23.3	456.8	1 614	176.9	26.35	79.25	7.27	2.46	0.49	91.5	8.5
WW005 (2)	m	adult	8	PB	76.7	23.3	442.1	1 669	162.4	26.63	71.25	6.88	2.67	0.83	91.0	9.0
WW058 (1)	f	adult	7	PM	87.6	12.4	447.7	1 209	213.4	26.55	78.25	10.74	2.27	0.89	92.1	7.9
WW061 (1)	f	adult	7	PM	87.0	13.0	498.7	1 249	171.1	28.88	91.25	9.09	2.22	0.66	92.9	7.1
WW301 (1)	m	adult	6	PM	80.8	19.2	636.4	1 338	223.6	35.92	82.25	12.56	3.19	0.99	91.8	8.2
YY039 (1)	f	adult	4	PM	84.1	15.9	424.1	1 369	145.8	25.72	81.25	10.08	2.00	0.51	92.8	7.2
YY070 (1)	f	adult	4	PB	86.7	13.3	399.8	1 149	124.3	21.78	70.25	7.03	2.01	0.64	91.6	8.4
YY096 (1)	f	subadult	2	PM	72.9	27.1	433.1	1 134	122.6	28.70	71.25	6.85	2.22	0.58	92.8	7.2
YY150 (1)	m	subadult	4	PM	87.3	12.7	501.1	1 646	229.6	20.08	84.25	8.49	2.56	1.22	92.0	8.0
YY189 (1)	f	subadult	2	PM	91.5	8.5	505.8	1 166	157.6	27.67	83.25	8.49	2.25	0.67	92.5	7.5
YY189 (2)	f	adult	3	PM	86.8	13.2	485.1	1 198	155.8	23.10	72.25	8.79	2.21	0.80	91.3	8.7
YY189 (3)	f	adult	4	PB	86.8	13.2	562	1 134	163.3	18.55	69.25	3.87	2.13	0.45	89.7	10.3
YY189 (4)	f	adult	4	PM	86.8	13.2	454.4	1 102	154.7	26.67	70.25	10.61	2.10	0.80	92.7	7.3
YY189 (5)	f	adult	5	PB	86.8	13.2	578.8	1 102	156.1	22.80	62.25	6.16	2.28	0.68	90.9	9.1
YY193 (1)	f	adult	4	PB	89.9	10.1	400.6	1 054	133	19.92	60.25	6.98	2.11	0.73	90.4	9.6
YY193 (2)	f	adult	4	PM	89.9	10.1	388.8	1 209	180.2	25.72	91.25	12.79	2.16	1.00	92.3	7.7
YY240 (1)	f	adult	4	PB	85.5	14.5	428	1 309	177.5	19.53	51.25	6.08	2.02	0.62	90.6	9.4
YY264 (1)	f	adult	4	PB	88.4	11.6	430.7	1 054	134.6	21.58	50.25	6.43	2.02	0.87	91.5	8.5
YY264 (2)	f	adult	4	PM	88.4	11.6	390.8	1 114	175.9	26.80	95.25	10.99	2.01	1.06	93.0	7.0

YY348 (1)	f	adult	4	PB	85.8	14.2	410.7	963.8	171	20.08	84.25	8.49	2.23	0.79	90.0	10.0
YY348 (2)	f	adult	4	PM	85.8	14.2	422.5	1 249	209.3	26.07	95.25	12.15	2.32	0.83	91.8	8.2
YY361 (1)	m	subadult	3	PM	89.2	10.8	498.2	1 449	199.4	26.03	79.25	10.07	1.96	0.57	93.0	7.0

Supplementary Figures

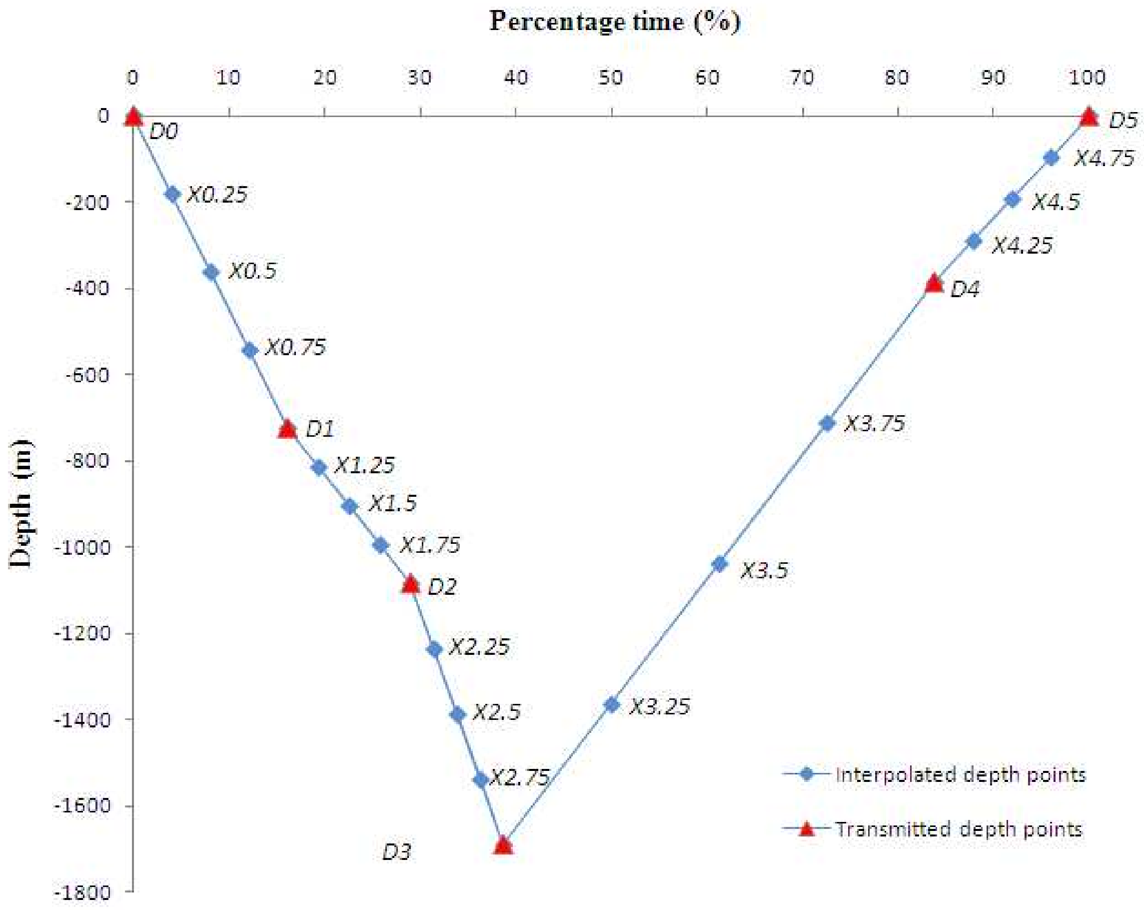
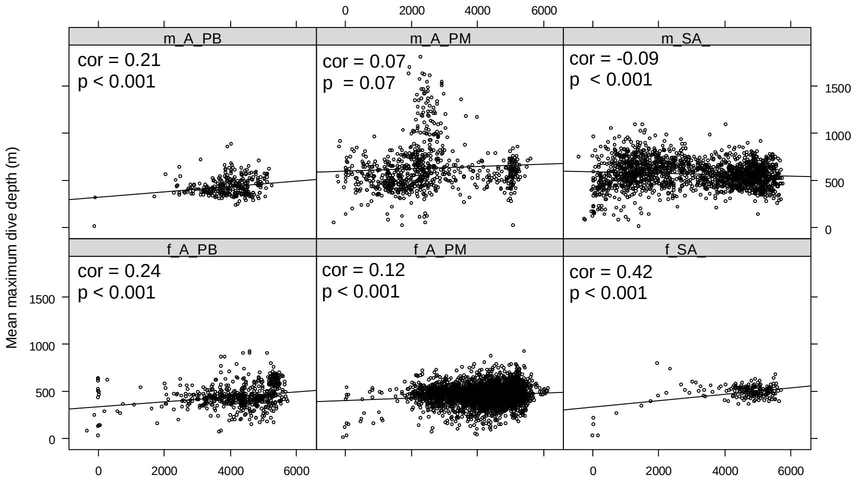
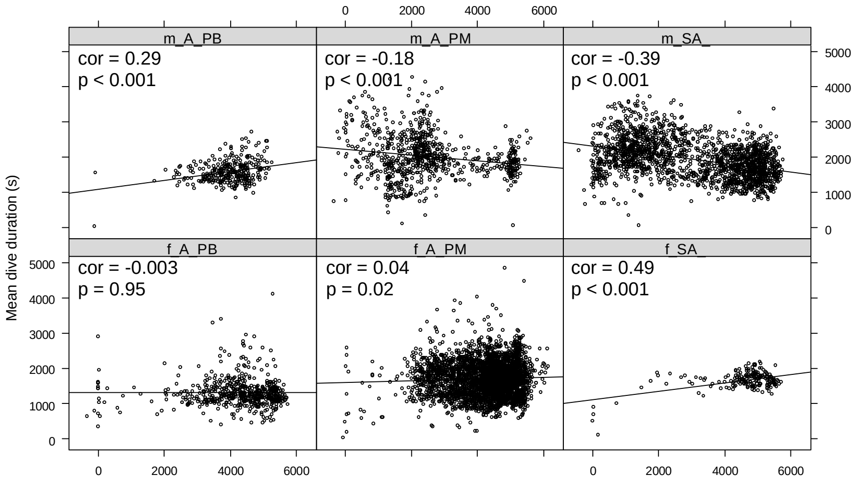


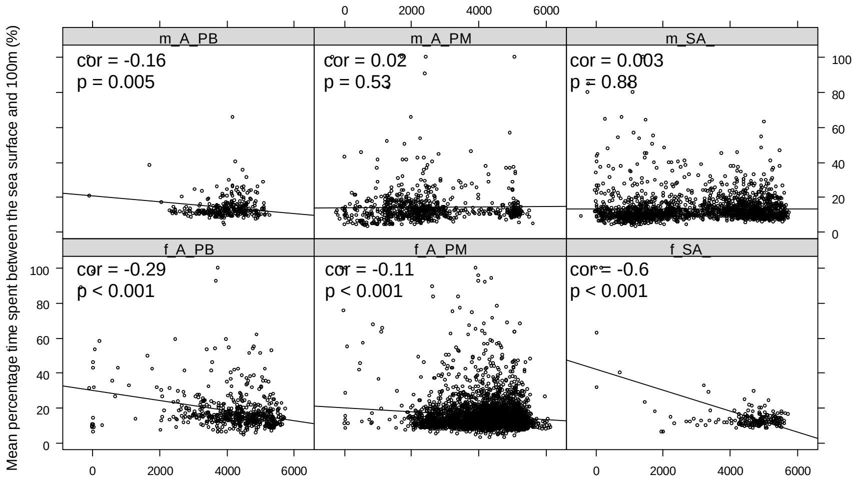
Figure A1. Figure indicating the creation of interpolated depth points, allowing for the estimation of time spent within depth bins. $D_{0\text{-}5}$ represent transmitted depth points. $X_{0.25\text{-}4.75}$ represent artificial interpolated depth points, assuming constant swim speeds and directions between the transmitted depth points.


m_A_PB
cor = 0.21
p < 0.001
m_A_PM
cor = 0.07
p = 0.07
m_SA_
cor = -0.09
p < 0.001
f_A_PB
cor = 0.24
p < 0.001
f_A_PM
cor = 0.12
p < 0.001
f_SA_
cor = 0.42
p < 0.001
Mean maximum dive depth (m)
Mean bottom depth (m)
0
500
1000
1500
0
2000
4000
6000

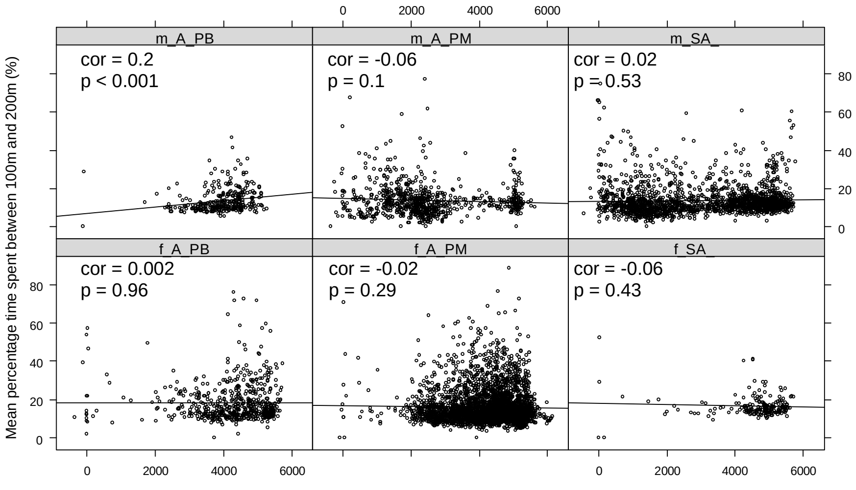
A


m_A_PB
cor = 0.29
p < 0.001
m_A_PM
cor = -0.18
p < 0.001
m_SA_
cor = -0.39
p < 0.001
f_A_PB
cor = -0.003
p = 0.95
f_A_PM
cor = 0.04
p = 0.02
f_SA_
cor = 0.49
p < 0.001
Mean dive duration (s)
Mean bottom depth (m)
0
1000
2000
3000
4000
5000
0
2000
4000
6000

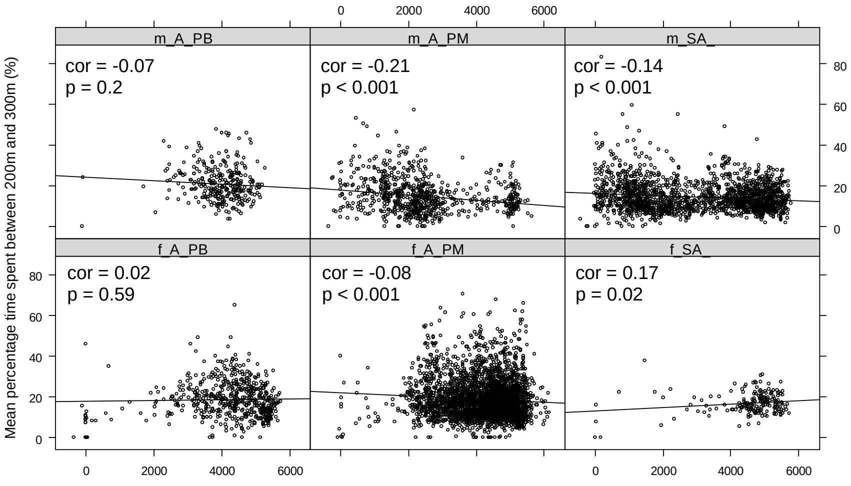
B


m_A_PB
cor = -0.16
p = 0.005
m_A_PM
cor = 0.02
p = 0.53
m_SA_
cor = 0.003
p = 0.88
f_A_PB
cor = -0.29
p < 0.001
f_A_PM
cor = -0.11
p < 0.001
f_SA_
cor = -0.6
p < 0.001
Mean percentage time spent between the sea surface and 100m (%)
Mean bottom depth (m)
0
20
40
60
80
100
0
2000
4000
6000

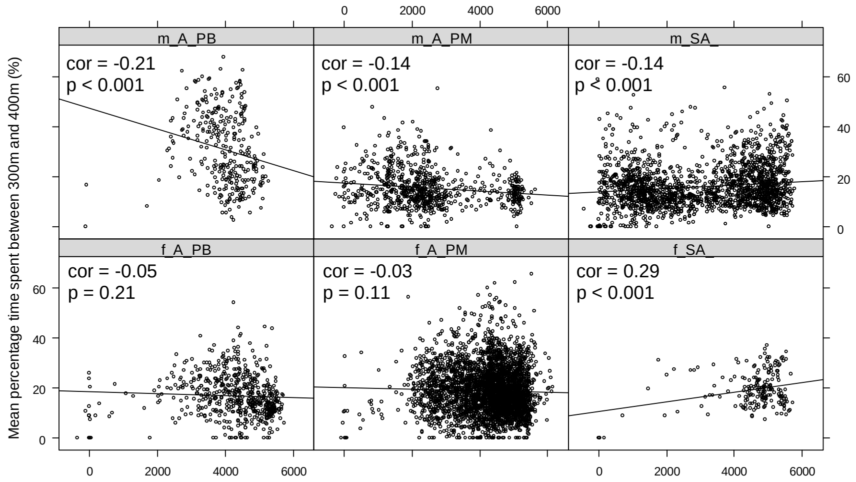
C


m_A_PB
cor = 0.2
p < 0.001
m_A_PM
cor = -0.06
p = 0.1
m_SA_
cor = 0.02
p = 0.53
f_A_PB
cor = 0.002
p = 0.96
f_A_PM
cor = -0.02
p = 0.29
f_SA_
cor = -0.06
p = 0.43
Mean percentage time spent between 100m and 200m (%)
Mean bottom depth (m)
0
20
40
60
80
0
2000
4000
6000

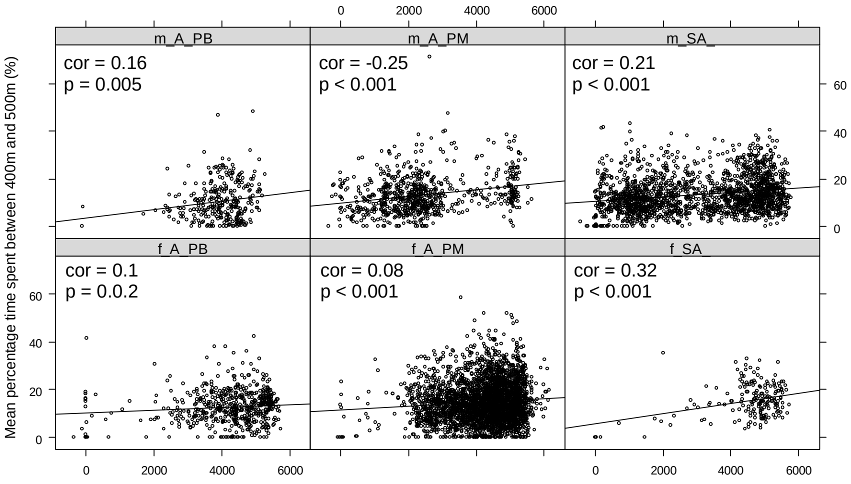
D


0
2000
4000
6000
m_A_PB
cor = -0.07
p = 0.2
m_A_PM
cor = -0.21
p < 0.001
m_SA_
cor = -0.14
p < 0.001
f_A_PB
cor = 0.02
p = 0.59
f_A_PM
cor = -0.08
p < 0.001
f_SA_
cor = 0.17
p = 0.02
0
20
40
60
80
Mean percentage time spent between 200m and 300m (%)
Mean bottom depth (m)

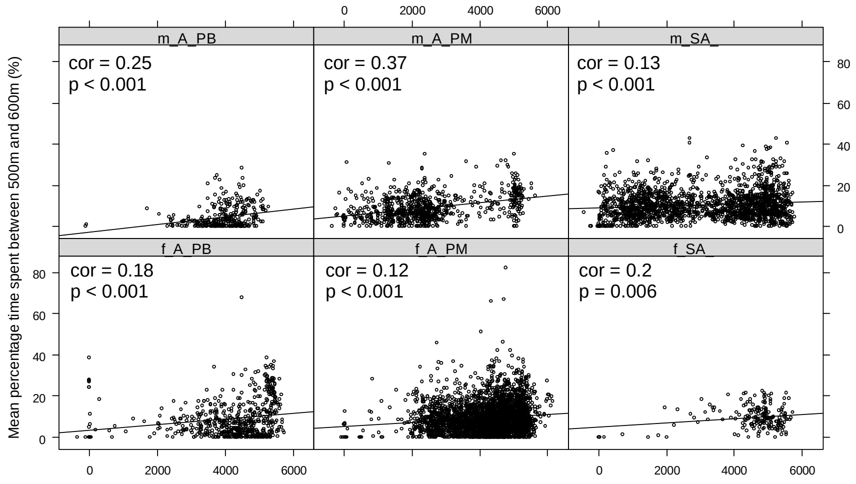
E


0
2000
4000
6000
m_A_PB
cor = -0.21
p < 0.001
m_A_PM
cor = -0.14
p < 0.001
m_SA_
cor = -0.14
p < 0.001
f_A_PB
cor = -0.05
p = 0.21
f_A_PM
cor = -0.03
p = 0.11
f_SA_
cor = 0.29
p < 0.001
0
20
40
60
Mean percentage time spent between 300m and 400m (%)
Mean bottom depth (m)

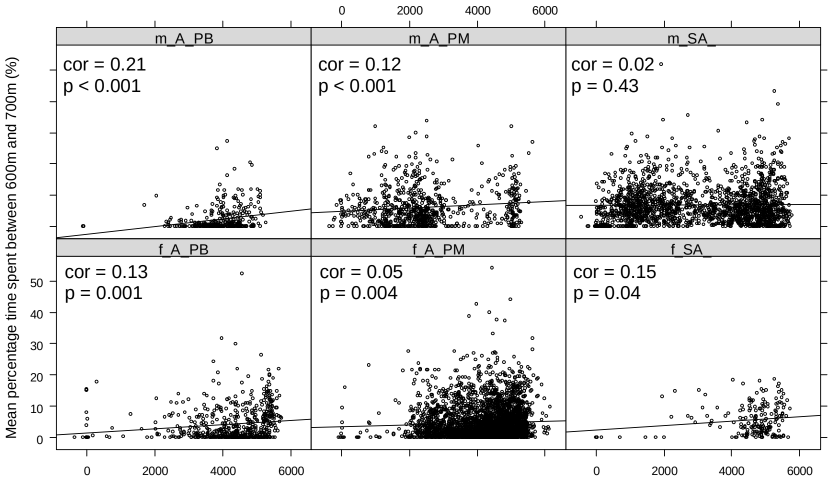
F


0
2000
4000
6000
m_A_PB
cor = 0.16
p = 0.005
m_A_PM
cor = -0.25
p < 0.001
m_SA_
cor = 0.21
p < 0.001
f_A_PB
cor = 0.1
p = 0.0.2
f_A_PM
cor = 0.08
p < 0.001
f_SA_
cor = 0.32
p < 0.001
0
20
40
60
Mean percentage time spent between 400m and 500m (%)
Mean bottom depth (m)

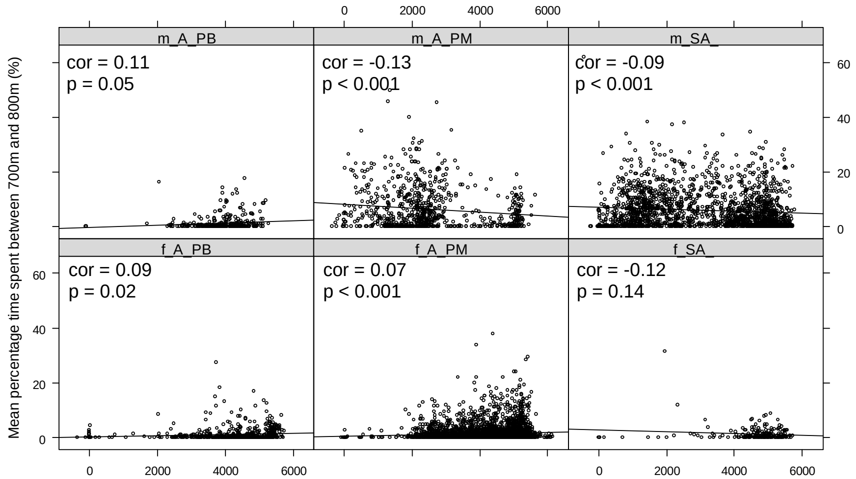
G


0
2000
4000
6000
m_A_PB
cor = 0.25
p < 0.001
m_A_PM
cor = 0.37
p < 0.001
m_SA_
cor = 0.13
p < 0.001
f_A_PB
cor = 0.18
p < 0.001
f_A_PM
cor = 0.12
p < 0.001
f_SA_
cor = 0.2
p = 0.006
0
20
40
60
80
Mean percentage time spent between 500m and 600m (%)
Mean bottom depth (m)

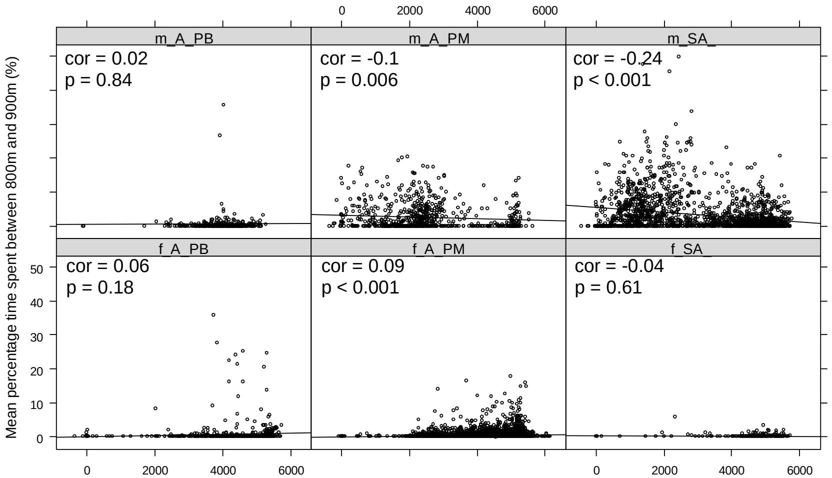
H


m_A_PB
cor = 0.21
p < 0.001
m_A_PM
cor = 0.12
p < 0.001
m_SA_
cor = 0.02
p = 0.43
f_A_PB
cor = 0.13
p = 0.001
f_A_PM
cor = 0.05
p = 0.004
f_SA_
cor = 0.15
p = 0.04
Mean percentage time spent between 600m and 700m (%)
Mean bottom depth (m)
0
2000
4000
6000
0
10
20
30
40
50

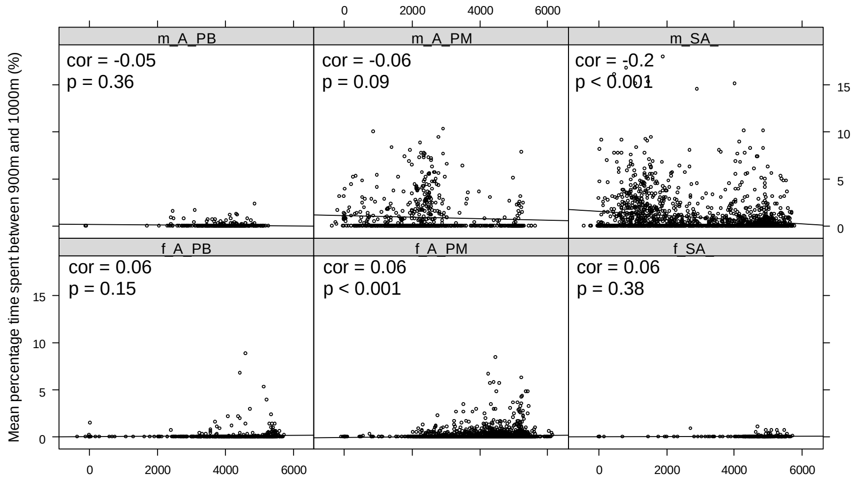
I


m_A_PB
cor = 0.11
p = 0.05
m_A_PM
cor = -0.13
p < 0.001
m_SA_
cor = -0.09
p < 0.001
f_A_PB
cor = 0.09
p = 0.02
f_A_PM
cor = 0.07
p < 0.001
f_SA_
cor = -0.12
p = 0.14
Mean percentage time spent between 700m and 800m (%)
Mean bottom depth (m)
0
2000
4000
6000
0
20
40
60

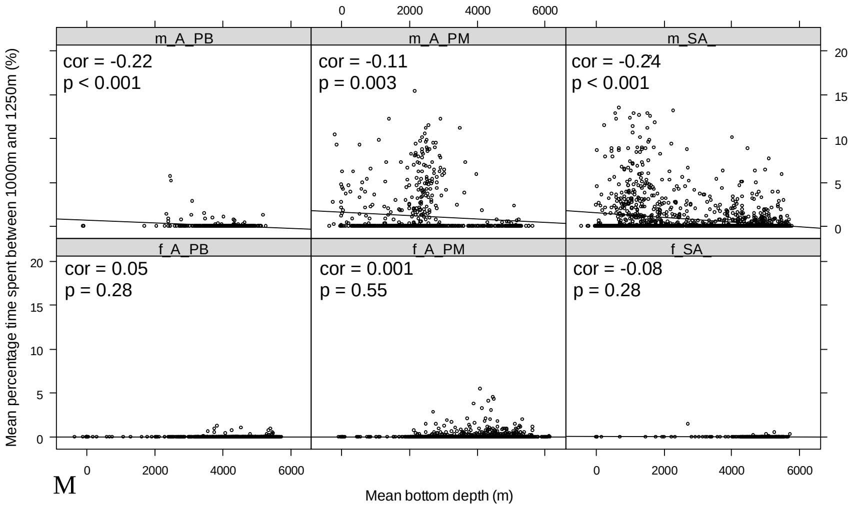
J


m_A_PB
cor = 0.02
p = 0.84
m_A_PM
cor = -0.1
p = 0.006
m_SA_
cor = -0.24
p < 0.001
f_A_PB
cor = 0.06
p = 0.18
f_A_PM
cor = 0.09
p < 0.001
f_SA_
cor = -0.04
p = 0.61
Mean percentage time spent between 800m and 900m (%)
Mean bottom depth (m)
0
2000
4000
6000
0
10
20
30
40
50

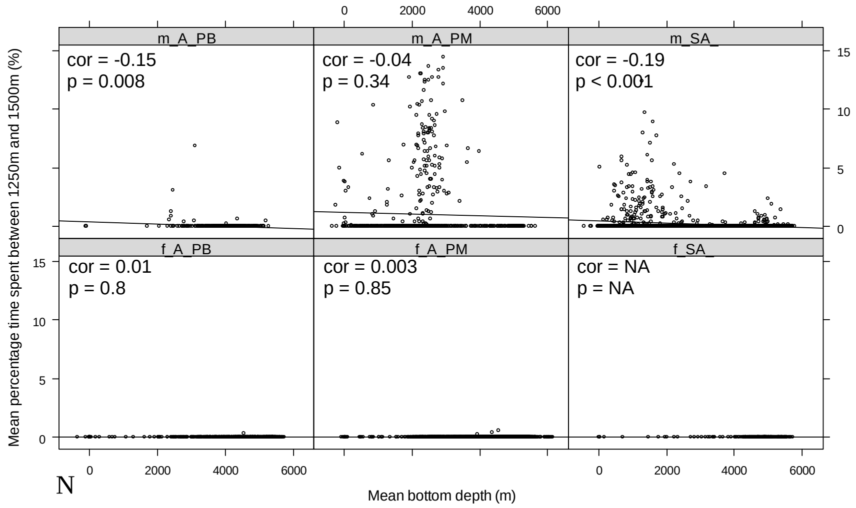
K


m_A_PB
cor = -0.05
p = 0.36
m_A_PM
cor = -0.06
p = 0.09
m_SA_
cor = -0.2
p < 0.001
f_A_PB
cor = 0.06
p = 0.15
f_A_PM
cor = 0.06
p < 0.001
f_SA_
cor = 0.06
p = 0.38
Mean percentage time spent between 900m and 1000m (%)
Mean bottom depth (m)
0
2000
4000
6000
0
5
10
15

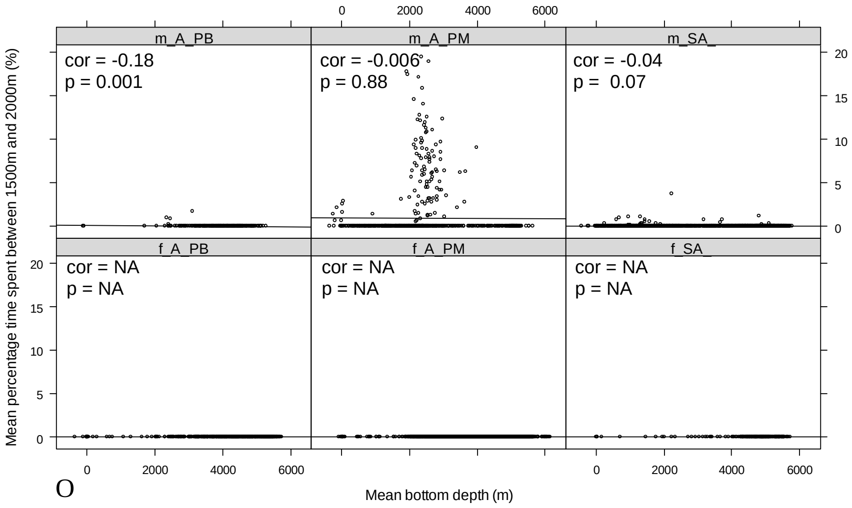
L


m_A_PB
cor = -0.22
p < 0.001
m_A_PM
cor = -0.11
p = 0.003
m_SA_
cor = -0.24
p < 0.001
f_A_PB
cor = 0.05
p = 0.28
f_A_PM
cor = 0.001
p = 0.55
f_SA_
cor = -0.08
p = 0.28
Mean percentage time spent between 1000m and 1250m (%)
Mean bottom depth (m)
0
2000
4000
6000
0
5
10
15
20

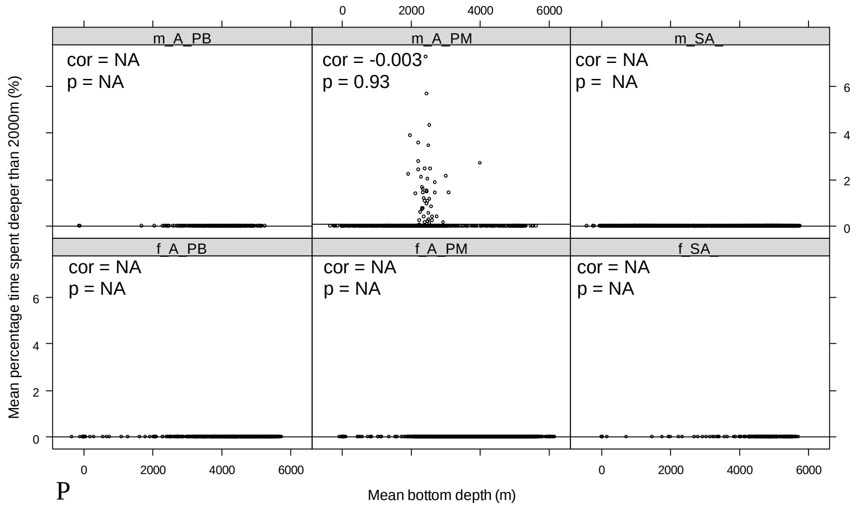
M


m_A_PB
cor = -0.15
p = 0.008
m_A_PM
cor = -0.04
p = 0.34
m_SA_
cor = -0.19
p < 0.001
f_A_PB
cor = 0.01
p = 0.8
f_A_PM
cor = 0.003
p = 0.85
f_SA_
cor = NA
p = NA
Mean percentage time spent between 1250m and 1500m (%)
Mean bottom depth (m)
0
2000
4000
6000
0
5
10
15

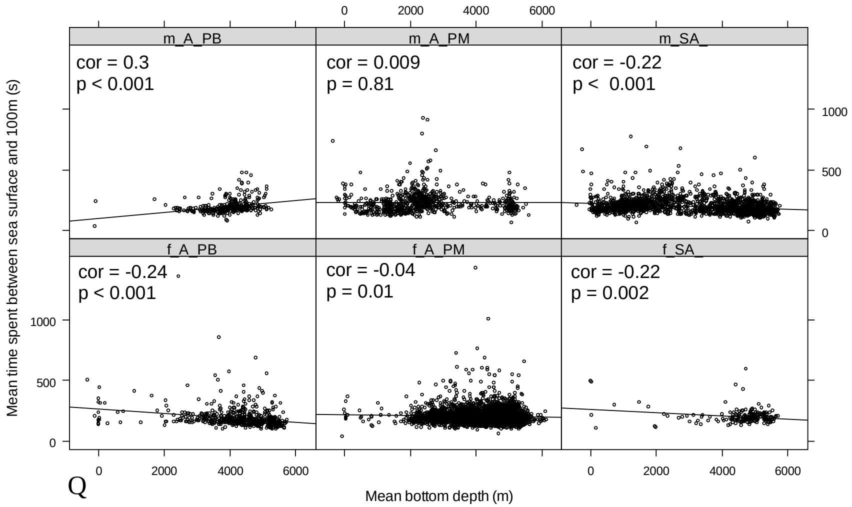
N


m_A_PB
cor = -0.18
p = 0.001
m_A_PM
cor = -0.006
p = 0.88
m_SA_
cor = -0.04
p = 0.07
f_A_PB
cor = NA
p = NA
f_A_PM
cor = NA
p = NA
f_SA_
cor = NA
p = NA
Mean percentage time spent between 1500m and 2000m (%)
Mean bottom depth (m)
0
2000
4000
6000
0
5
10
15
20

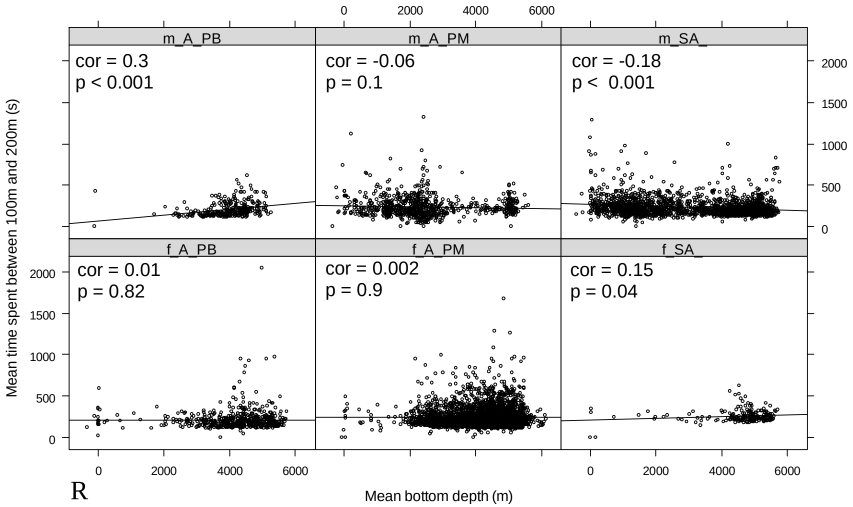
O


m_A_PB
cor = NA
p = NA
m_A_PM
cor = -0.003
p = 0.93
m_SA_
cor = NA
p = NA
f_A_PB
cor = NA
p = NA
f_A_PM
cor = NA
p = NA
f_SA_
cor = NA
p = NA
Mean percentage time spent deeper than 2000m (%)
Mean bottom depth (m)
0
2000
4000
6000
0
2
4
6

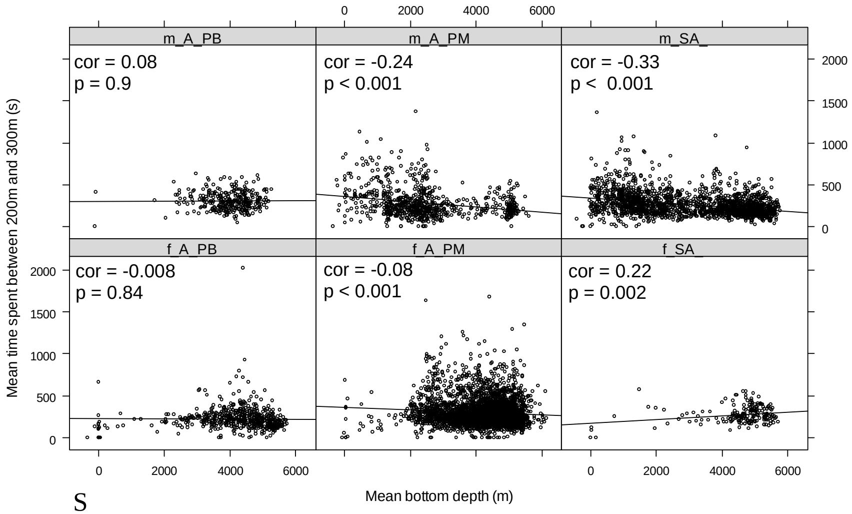
P


0
2000
4000
6000
m_A_PB
m_A_PM
m_SA_
cor = 0.3
p < 0.001
cor = 0.009
p = 0.81
cor = -0.22
p < 0.001
1000
500
0
f_A_PB
f_A_PM
f_SA_
cor = -0.24
p < 0.001
cor = -0.04
p = 0.01
cor = -0.22
p = 0.002
Mean time spent between sea surface and 100m (s)
1000
500
0
0
2000
4000
6000
0
2000
4000
6000
Mean bottom depth (m)

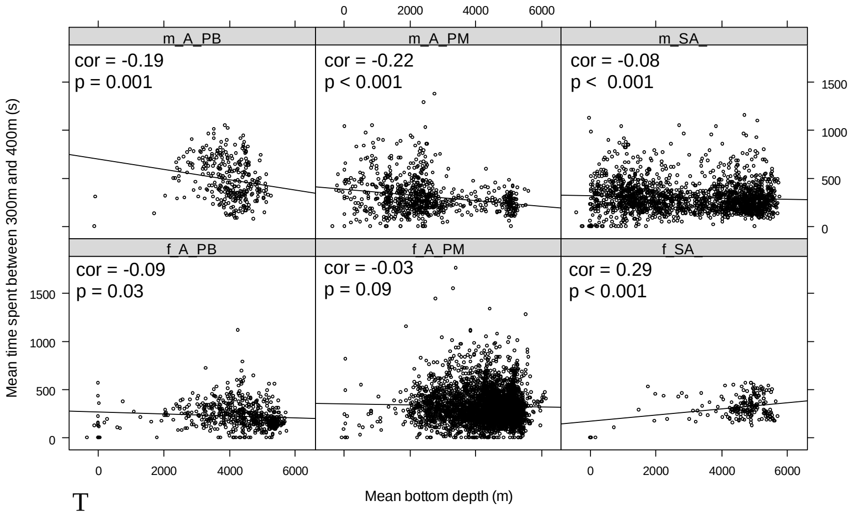
Q


0
2000
4000
6000
m_A_PB
m_A_PM
m_SA_
cor = 0.3
p < 0.001
cor = -0.06
p = 0.1
cor = -0.18
p < 0.001
2000
1500
1000
500
0
f_A_PB
f_A_PM
f_SA_
cor = 0.01
p = 0.82
cor = 0.002
p = 0.9
cor = 0.15
p = 0.04
Mean time spent between 100m and 200m (s)
2000
1500
1000
500
0
0
2000
4000
6000
0
2000
4000
6000
Mean bottom depth (m)

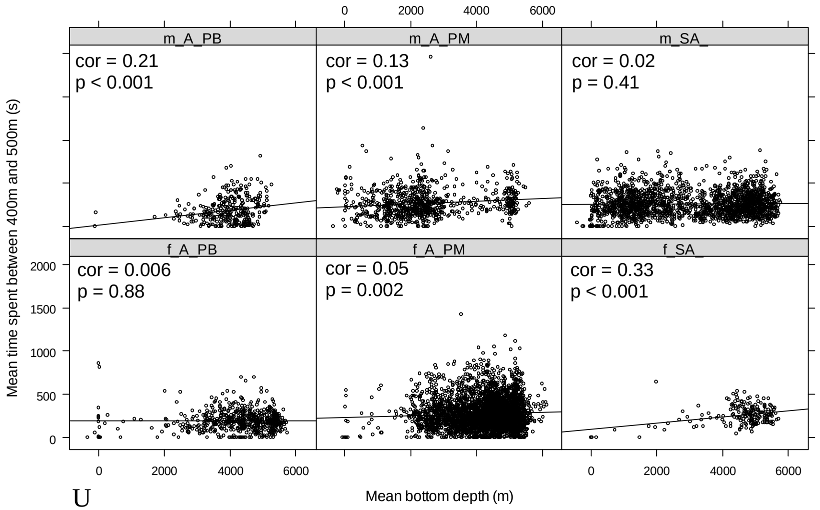
R


0
2000
4000
6000
m_A_PB
m_A_PM
m_SA_
cor = 0.08
p = 0.9
cor = -0.24
p < 0.001
cor = -0.33
p < 0.001
2000
1500
1000
500
0
f_A_PB
f_A_PM
f_SA_
cor = -0.008
p = 0.84
cor = -0.08
p < 0.001
cor = 0.22
p = 0.002
Mean time spent between 200m and 300m (s)
2000
1500
1000
500
0
0
2000
4000
6000
0
2000
4000
6000
Mean bottom depth (m)

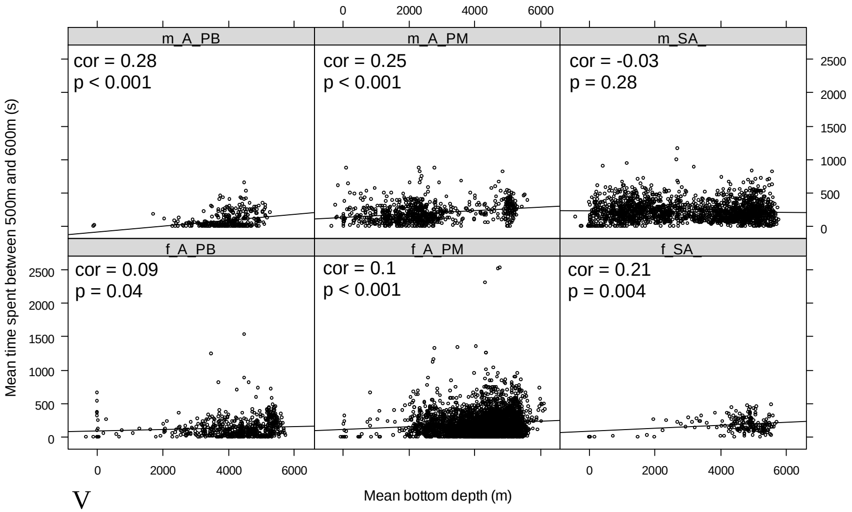
S


0
2000
4000
6000
m_A_PB
m_A_PM
m_SA_
cor = -0.19
p = 0.001
cor = -0.22
p < 0.001
cor = -0.08
p < 0.001
1500
1000
500
0
f_A_PB
f_A_PM
f_SA_
cor = -0.09
p = 0.03
cor = -0.03
p = 0.09
cor = 0.29
p < 0.001
Mean time spent between 300m and 400m (s)
1500
1000
500
0
0
2000
4000
6000
0
2000
4000
6000
Mean bottom depth (m)

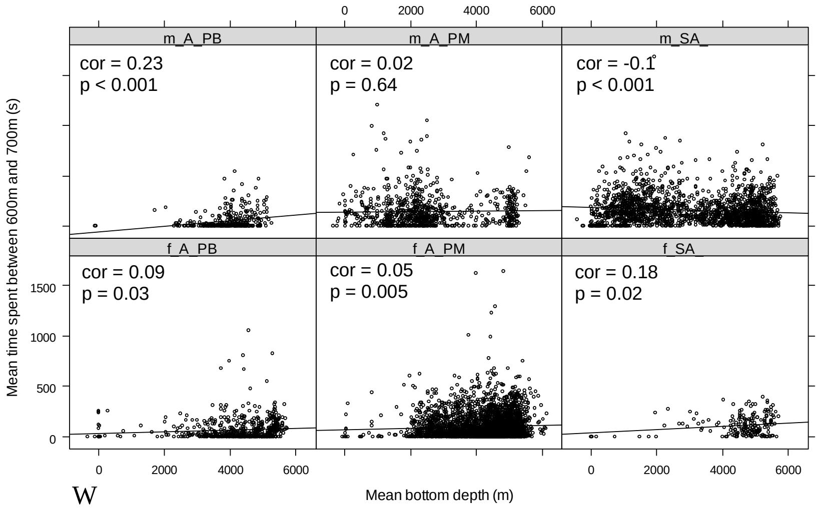
T


m_A_PB
cor = 0.21
p < 0.001
m_A_PM
cor = 0.13
p < 0.001
m_SA_
cor = 0.02
p = 0.41
f_A_PB
cor = 0.006
p = 0.88
f_A_PM
cor = 0.05
p = 0.002
f_SA_
cor = 0.33
p < 0.001
0
2000
4000
6000
0
500
1000
1500
2000
Mean time spent between 400m and 500m (s)
Mean bottom depth (m)

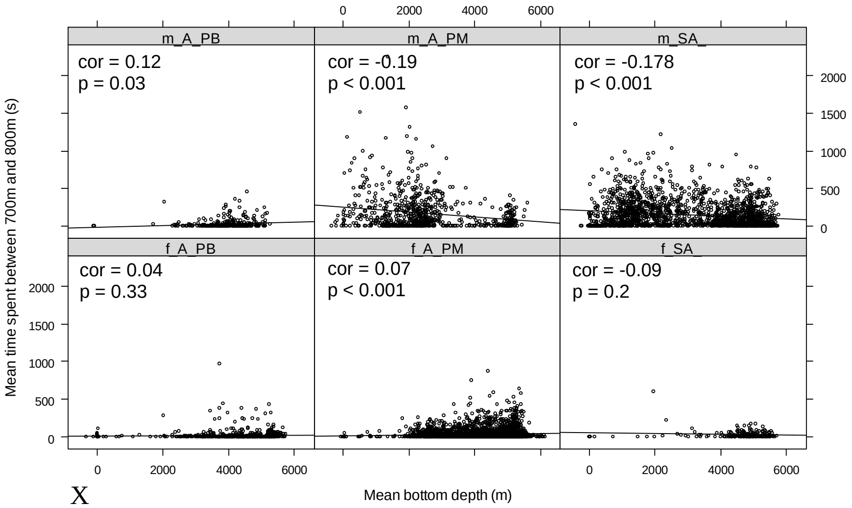
U


m_A_PB
cor = 0.28
p < 0.001
m_A_PM
cor = 0.25
p < 0.001
m_SA_
cor = -0.03
p = 0.28
f_A_PB
cor = 0.09
p = 0.04
f_A_PM
cor = 0.1
p < 0.001
f_SA_
cor = 0.21
p = 0.004
0
2000
4000
6000
0
500
1000
1500
2000
2500
Mean time spent between 500m and 600m (s)
Mean bottom depth (m)

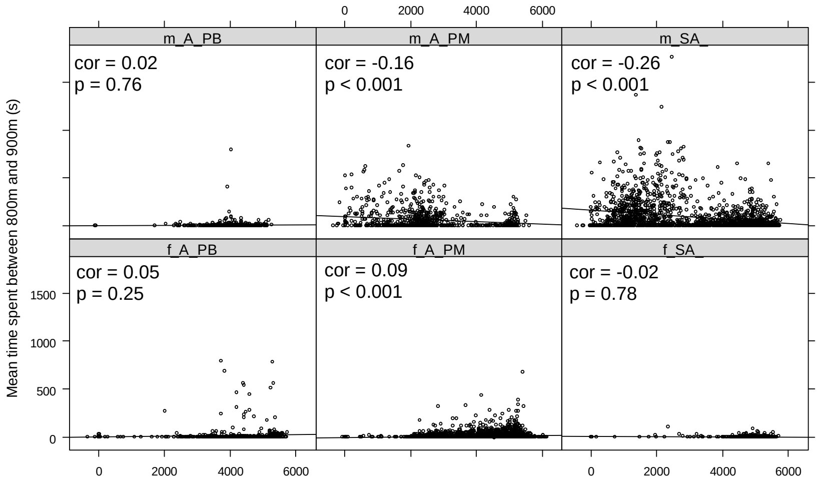
V


m_A_PB
cor = 0.23
p < 0.001
m_A_PM
cor = 0.02
p = 0.64
m_SA_
cor = -0.1
p < 0.001
f_A_PB
cor = 0.09
p = 0.03
f_A_PM
cor = 0.05
p = 0.005
f_SA_
cor = 0.18
p = 0.02
0
2000
4000
6000
0
500
1000
1500
Mean time spent between 600m and 700m (s)
Mean bottom depth (m)

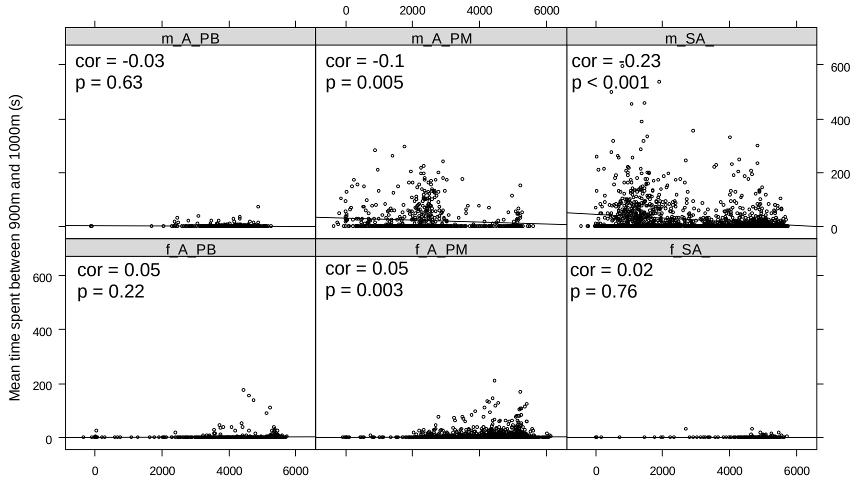
W


m_A_PB
cor = 0.12
p = 0.03
m_A_PM
cor = -0.19
p < 0.001
m_SA_
cor = -0.178
p < 0.001
f_A_PB
cor = 0.04
p = 0.33
f_A_PM
cor = 0.07
p < 0.001
f_SA_
cor = -0.09
p = 0.2
0
2000
4000
6000
0
500
1000
1500
2000
Mean time spent between 700m and 800m (s)
Mean bottom depth (m)

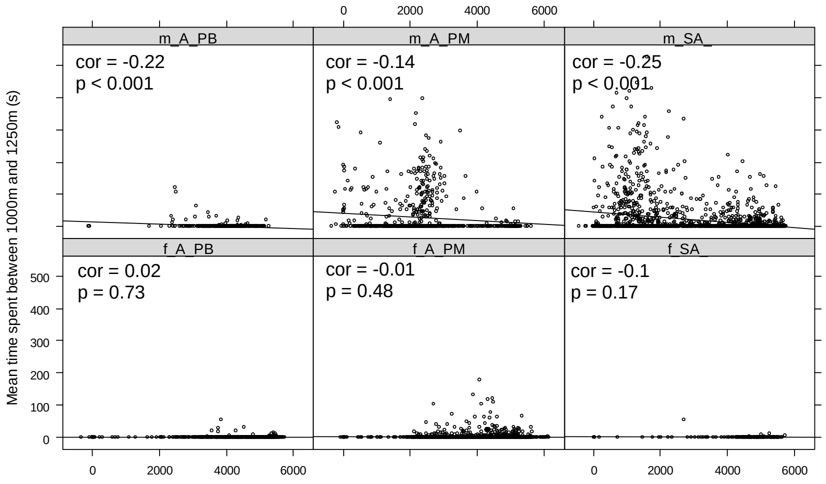
X


m_A_PB
cor = 0.02
p = 0.76
m_A_PM
cor = -0.16
p < 0.001
m_SA_
cor = -0.26
p < 0.001
f_A_PB
cor = 0.05
p = 0.25
f_A_PM
cor = 0.09
p < 0.001
f_SA_
cor = -0.02
p = 0.78
0
500
1000
1500
0
2000
4000
6000
Mean time spent between 800m and 900m (s)
Mean bottom depth (m)

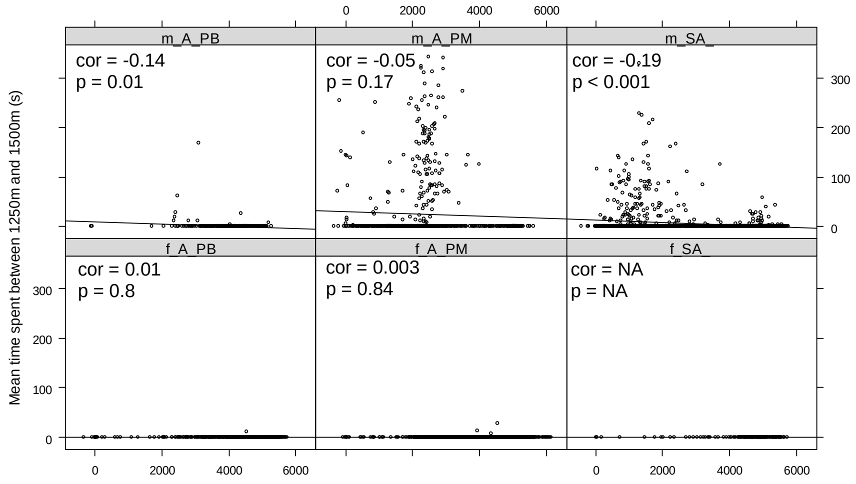
Y


m_A_PB
cor = -0.03
p = 0.63
m_A_PM
cor = -0.1
p = 0.005
m_SA_
cor = -0.23
p < 0.001
f_A_PB
cor = 0.05
p = 0.22
f_A_PM
cor = 0.05
p = 0.003
f_SA_
cor = 0.02
p = 0.76
0
200
400
600
0
2000
4000
6000
Mean time spent between 900m and 1000m (s)
Mean bottom depth (m)

Z


m_A_PB
cor = -0.22
p < 0.001
m_A_PM
cor = -0.14
p < 0.001
m_SA_
cor = -0.25
p < 0.001
f_A_PB
cor = 0.02
p = 0.73
f_A_PM
cor = -0.01
p = 0.48
f_SA_
cor = -0.1
p = 0.17
0
100
200
300
400
500
0
2000
4000
6000
Mean time spent between 1000m and 1250m (s)
Mean bottom depth (m)

AA


m_A_PB
cor = -0.14
p = 0.01
m_A_PM
cor = -0.05
p = 0.17
m_SA_
cor = -0.19
p < 0.001
f_A_PB
cor = 0.01
p = 0.8
f_A_PM
cor = 0.003
p = 0.84
f_SA_
cor = NA
p = NA
0
100
200
300
0
2000
4000
6000
Mean time spent between 1250m and 1500m (s)
Mean bottom depth (m)

AB

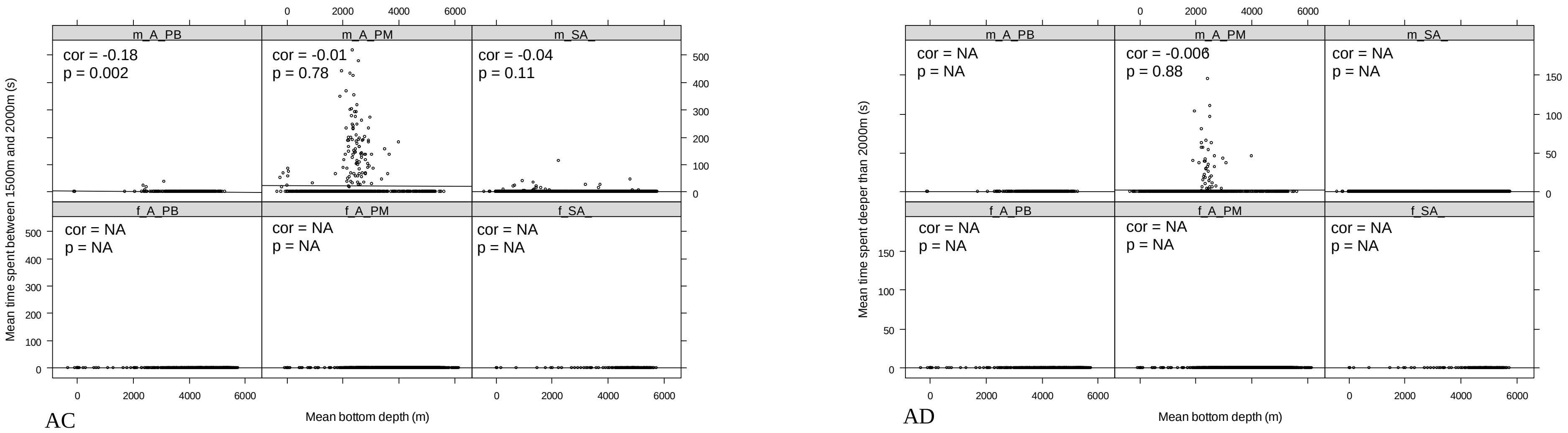
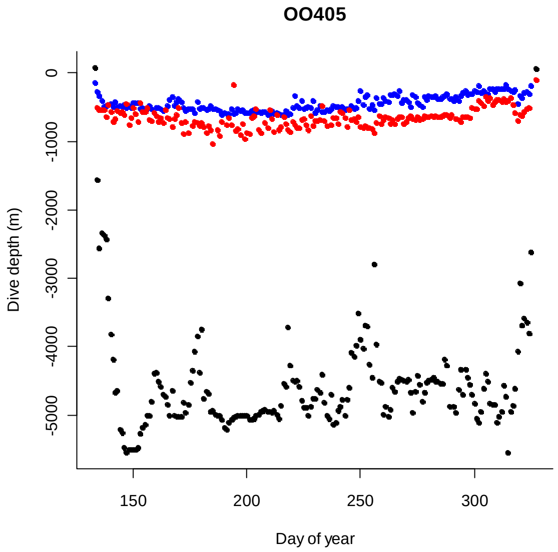
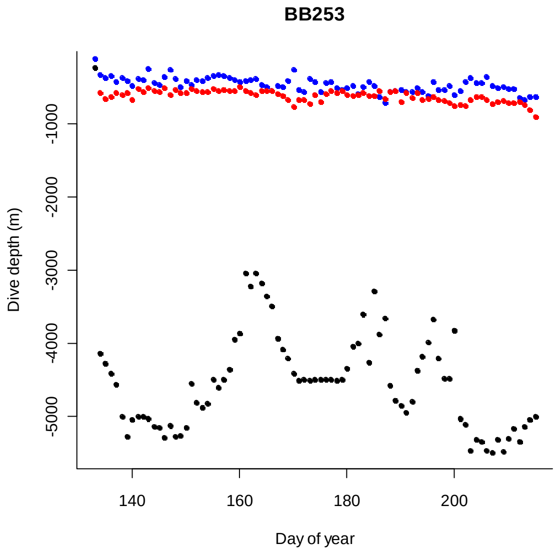
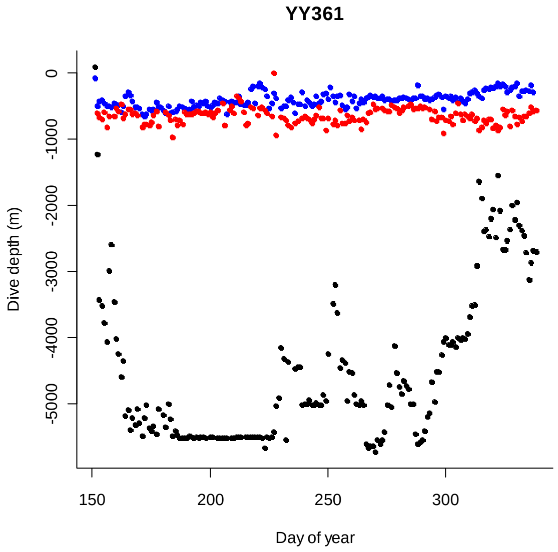


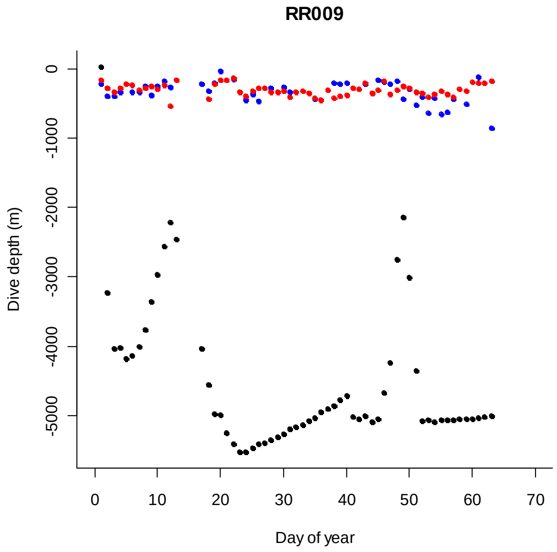
Figure A2: Correlation plots, indicating the relationships between various dive parameters (A – AD) and estimated water depth for different age- and sex classes. m_A_PB = adult males on post-breeding migrations; m_A_PM = adult males on post-moult migrations; sam = subadult males; f_A_PB = adult females on post-breeding migrations; f_A_PM = adult females on post-moult migrations; saf = subadult females. Plots are labelled as follows: A = mean maximum dive depth; B = mean dive duration; C-P = mean percentage time spent in various depth categories ($PT_{0\text{-}100m}$ – PT_{2000+m}); Q-AD = mean actual time (s) spent in various depth categories ($TT_{0\text{-}100m}$ – TT_{2000+m}).

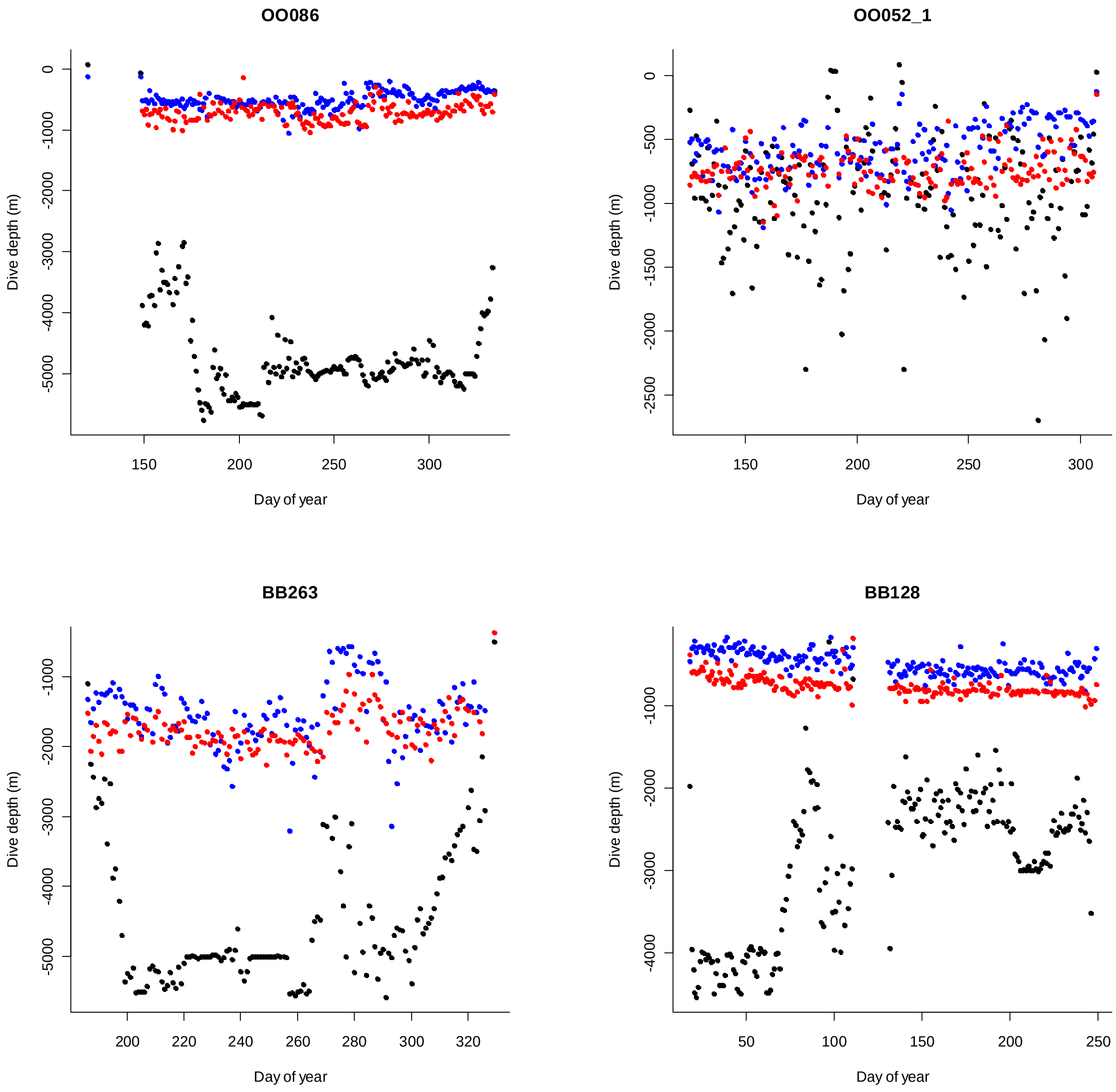
APPENDIX B: SUPPLEMENTARY MATERIAL FOR CHAPTER 4

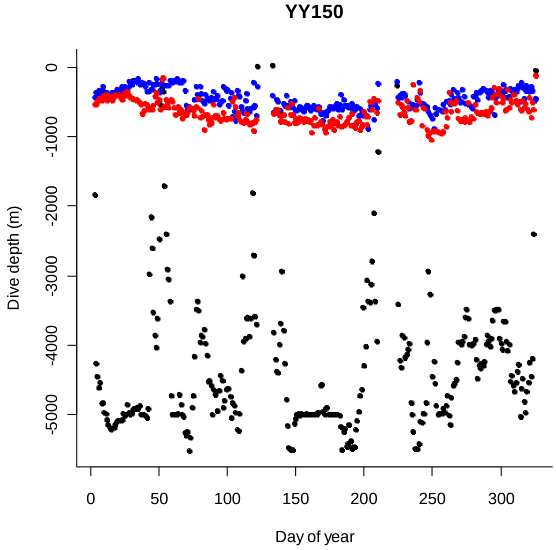


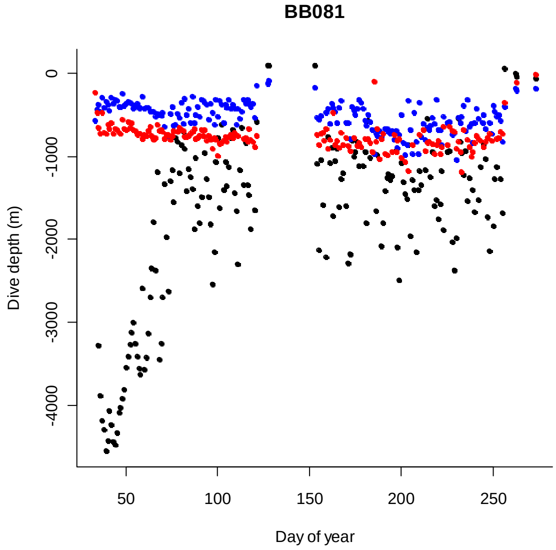


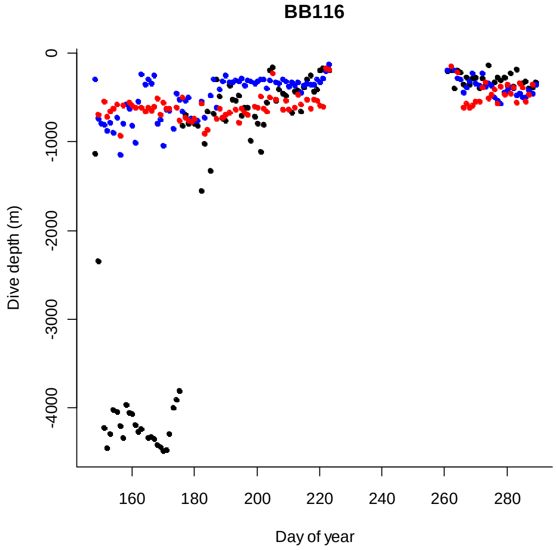


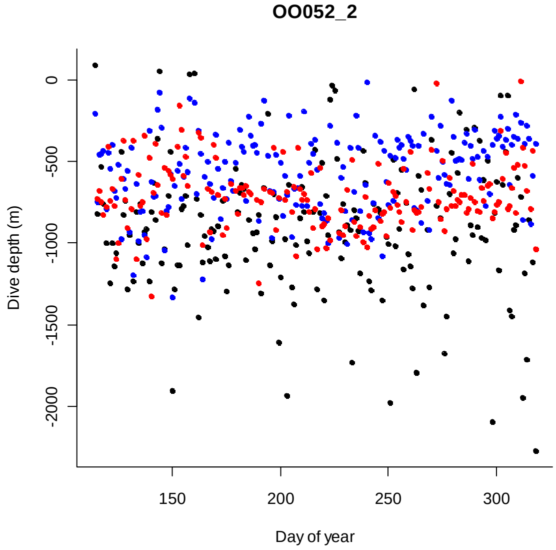


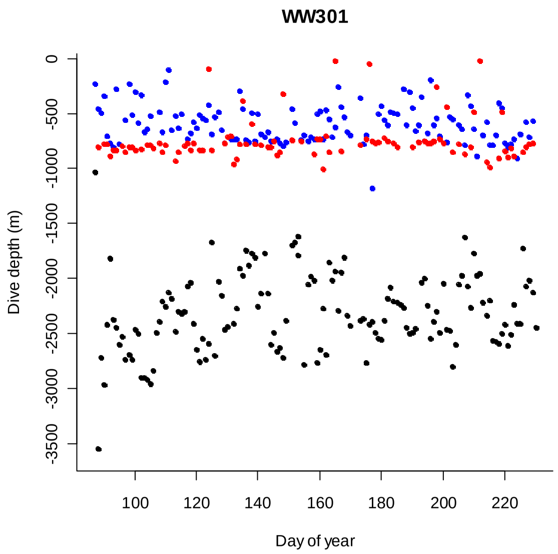

OO086
Dive depth (m)
0
-1000
-2000
-3000
-4000
-5000
150
200
250
300
Day of year
OO052_1
Dive depth (m)
0
-500
-1000
-1500
-2000
-2500
150
200
250
300
Day of year
BB263
Dive depth (m)
-1000
-2000
-3000
-4000
-5000
200
220
240
260
280
300
320
Day of year
BB128
Dive depth (m)
-1000
-2000
-3000
-4000
50
100
150
200
250
Day of year

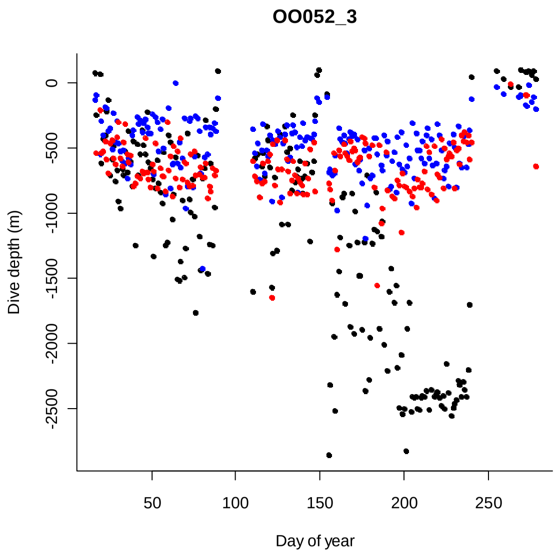

YY150
Dive depth (m)
0
-1000
-2000
-3000
-4000
-5000
0
50
100
150
200
250
300
Day of year

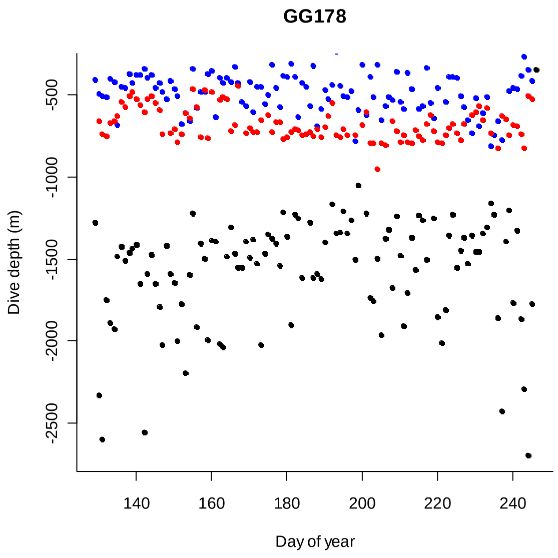

BB081
Dive depth (m)
0
-1000
-2000
-3000
-4000
50
100
150
200
250
Day of year

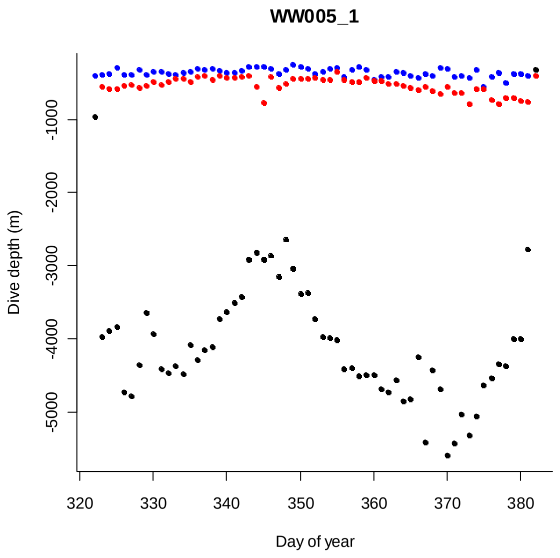

BB116
Dive depth (m)
0
-1000
-2000
-3000
-4000
160
180
200
220
240
260
280
Day of year

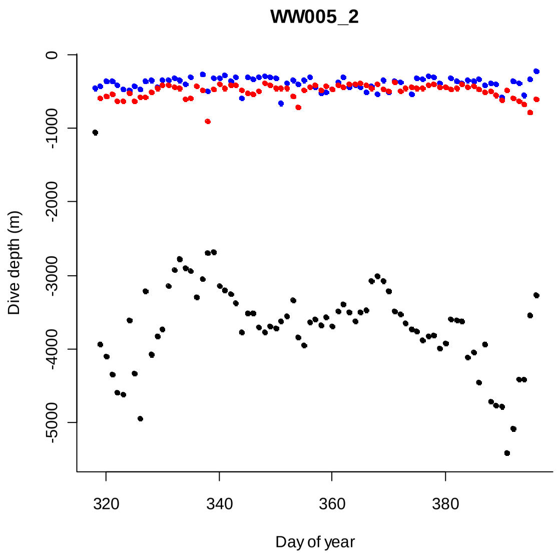

OO052_2
Dive depth (m)
0
-500
-1000
-1500
-2000
150
200
250
300
Day of year

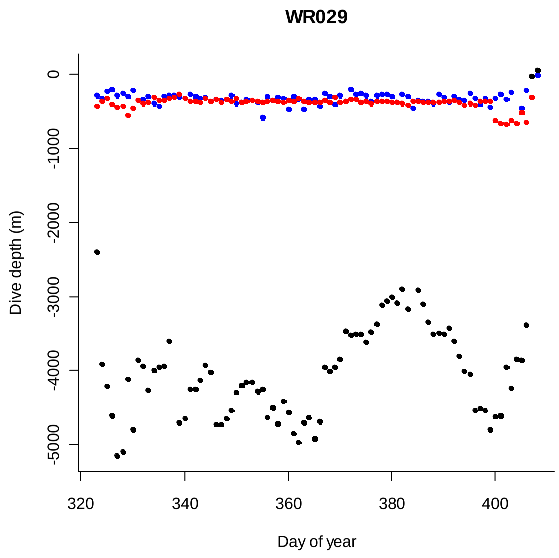

WW301
Dive depth (m)
0
-500
-1000
-1500
-2000
-2500
-3000
-3500
100
120
140
160
180
200
220
Day of year

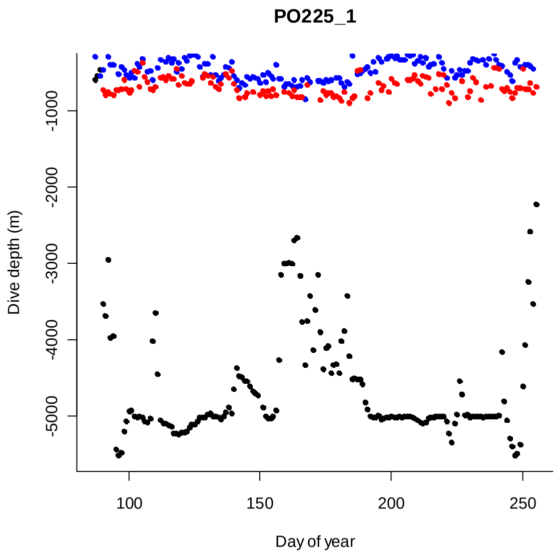

OO052_3
Dive depth (m)
0
-500
-1000
-1500
-2000
-2500
50
100
150
200
250
Day of year

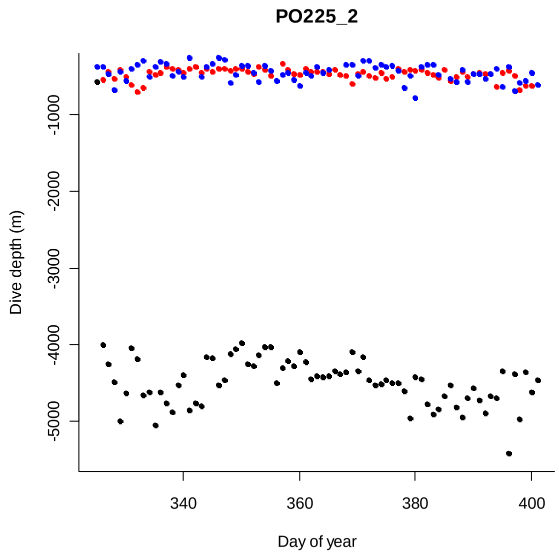

GG178
Dive depth (m)
-500
-1000
-1500
-2000
-2500
140
160
180
200
220
240
Day of year


WW005_1
Dive depth (m)
-1000
-2000
-3000
-4000
-5000
320
330
340
350
360
370
380
Day of year


WW005_2
Dive depth (m)
0
-1000
-2000
-3000
-4000
-5000
320
340
360
380
Day of year


WR029
Dive depth (m)
0
-1000
-2000
-3000
-4000
-5000
320
340
360
380
400
Day of year


PO225_1
Dive depth (m)
-1000
-2000
-3000
-4000
-5000
100
150
200
250
Day of year


PO225_2
Dive depth (m)
-1000
-2000
-3000
-4000
-5000
340
360
380
400
Day of year

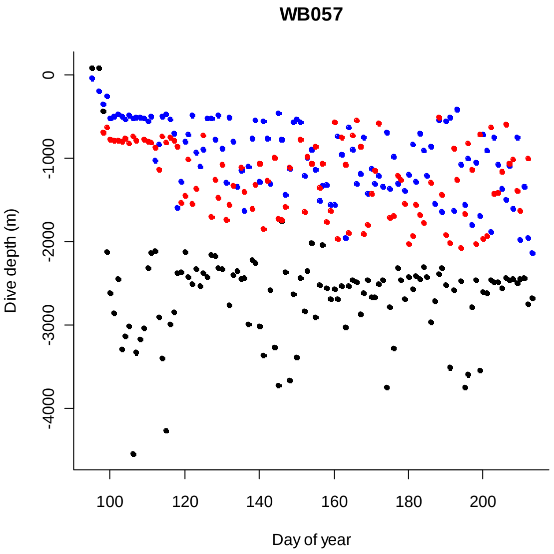


Figure B1: Time series scatterplots indicating the daily mean dive depths recorded for all male elephant seals during the day and at night in relation to estimates of bottom depth. Red dots = mean daytime dive depths (m); blue dots = mean night-time dive depths (m); black dots = estimates of bottom depth (m) for daily averaged location obtained through the Gebco atlas (IOC et al. 2003).