CHAPTER 1

GENERAL INTRODUCTION

Introduction

A thorough understanding of population processes and ecosystem functioning is vital in a world where biodiversity is threatened by climate change, habitat loss, overexploitation, or impacts from introduced species to name a few (Diamond 1984, Caughley 1994, Roberts and Hawkins 1999, Jones *et al.* 2003, Thomas *et al.* 2004). Conservation biology deals with small or declining populations (Caughley 1994) and at a population level, time series abundance data allow assessment of not only the conservation status, but also the intrinsic and extrinsic factors driving population trends of species (McMahon *et al.* 2005a, 2009). For long-lived species, long-term data is required to allow robust conclusions concerning temporal variation in abundance without sampling error caused by short-term population fluctuations (Barbraud *et al.* 2008). Several long-term time series abundance data of marine apex predators in the southern Indian Ocean for example, have indicated that populations have decreased (or in some cases increased) during the last half of the 1900's, probably in response to a regime shift in food availability (Weimerskirch *et al.* 2003). These studies of population abundance have signaled important changes that have occurred in the marine ecosystem (Weimerskirch *et al.* 2003), relevant to both conservation and management strategies in the region.

While population abundance data are useful to monitor population trends, more detailed complementary information on the population demography of the component species can be obtained by individually based long-term, longitudinal mark-recapture studies (Lebreton *et al.* 1992, Clobert *et al.* 1994). Demographic data may, for example, improve model predictions concerning the response of populations to changing environmental conditions (Keith *et al.* 2008). Generally, the focal point of long-term mark-recapture experiments is survival and fecundity of individuals or groups of individuals with particular traits, and how these vital rates vary through time and space (Lebreton *et al.* 1992). As survival and fecundity represent fitness, these rates are important components in many biological investigations. Consequently, mark-recapture experiments commonly form the cornerstone of investigations into population biology, including life history, population dynamics, regulation, behaviour, adaptation, physiology and movement (e.g., red deer *Cervus elaphus* [Coulson *et al.* 1997],

bighorn sheep *Ovis canadensis* [Coltman *et al.* 2002] and Soay sheep *Ovis aries* [Clutton-Brock and Pemberton 2004]).

The Southern Ocean is a highly dynamic environment that varies spatially in productivity, influencing the distribution and abundance of biological communities (Constable *et al.* 2003). Pelagic predators are abundant, although population numbers have fluctuated dramatically in the last century due to overexploitation (Laws 1977) and environmental change (Weimerskirch *et al.* 2003). Bird (Barbraud and Weimerskirch 2001, Croxall *et al.* 2002, Jenouvrier *et al.* 2005) and seal (Forcada *et al.* 2005, McMahon and Burton 2005) populations have been used as indicators of marine ecosystem health as their demography and population abundances are directly affected by the availability of their lower trophic level prey, which are themselves influenced by climatic and abiotic elements (Croxall *et al.* 1999). Populations of one such species, the southern elephant seal *Mirounga leonina* L., declined consistently across large parts of its range between the 1950s and 1990s (McMahon *et al.* 2005a). The small, well-studied southern elephant seal breeding population at Marion Island in the southern Indian Ocean is the focus of this dissertation.

Southern elephant seals (*Mirounga leonina*)

Pinnipeds (Order Carnivora, Suborder Pinnipedia) are carnivorous marine mammals comprising the families Phocidae (the true seals), Otariidae (the fur seals and sea lions), and Odobenidae (the walrus). Elephant seals (*Mirounga* spp.*)* are the largest living pinnipeds and belong to the family Phocidae. Two species are recognised: the northern elephant seal *M. angustirostris* and the southern elephant seal *M. leonina* (Le Boeuf and Laws 1994). Southern elephant seals are wide-ranging apex marine predators with a circumpolar distribution in the Southern Ocean (McMahon *et al.* 2005a). All seals migrate annually between terrestrial haulout sites (where they may breed, moult or winter) and pelagic foraging areas, but despite long range foraging migrations, most elephant seals are philopatric and return to their natal islands to haul out (Nicholls 1970, Hofmeyr 2000). Despite some gene flow between distant populations (Slade *et al.* 1998, Fabiani *et al.* 2003), the high site fidelity of elephant seals results in limited exchange of breeding individuals between major populations and four genetically distinct geographical provinces are recognized: the South Georgia province in the southern Atlantic Ocean, the Macquarie province in the southern Pacific Ocean, the Kerguelen province in the southern Indian Ocean and the Peninsula Valdés population on the Argentinean coast in the southern Atlantic Ocean (the only continental breeding population)

(Laws 1994, McMahon *et al.* 2005a). The global circumpolar breeding distribution of southern elephant seals is given in Figure 1.1.
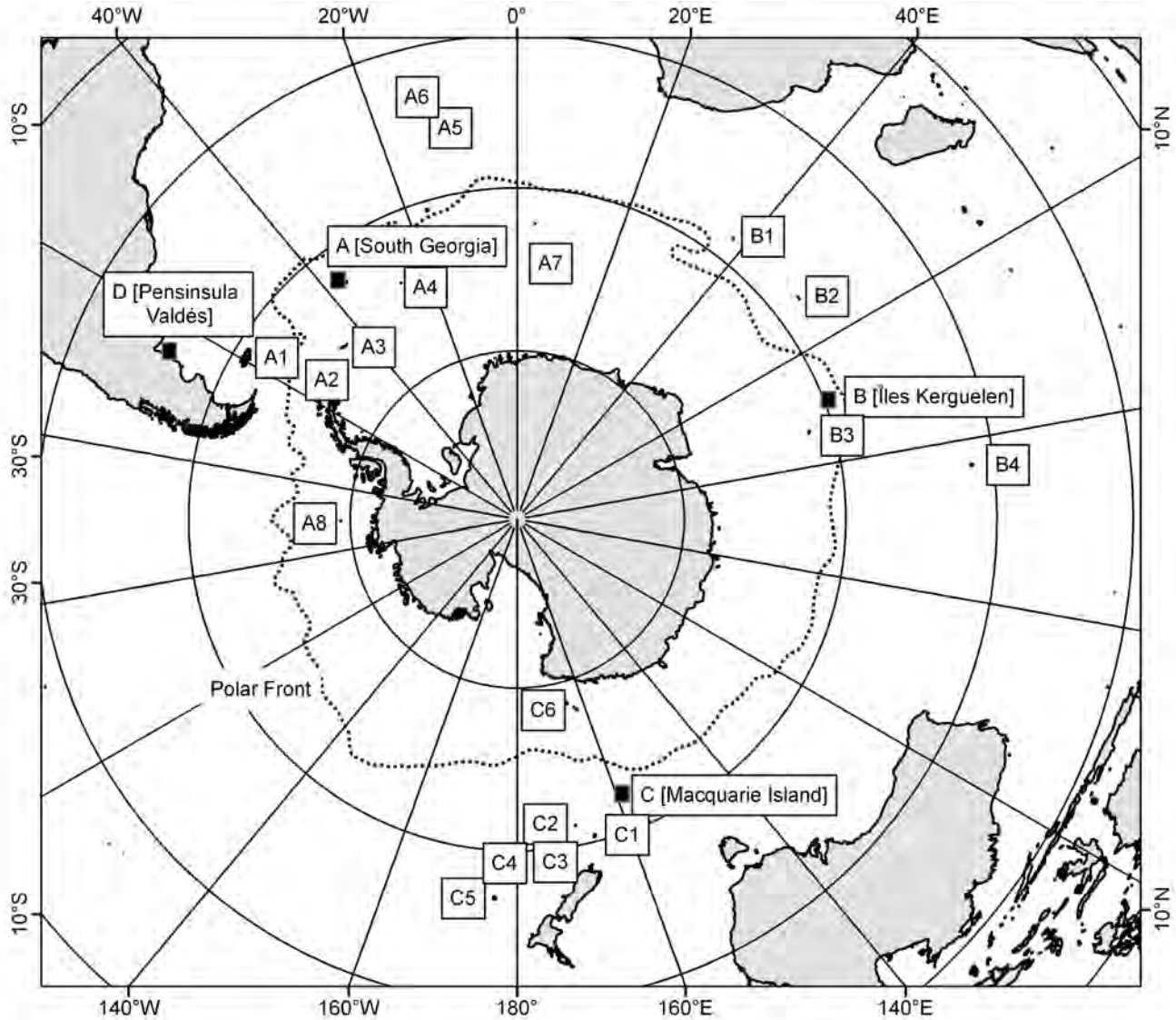

Figure 1.1. The circumpolar breeding distribution of southern elephant seals Mirounga leonina (Laws 1994, McMahon et al. 2005a). The four major populations (dark squares) of southern elephant seals in each geographical province and sub-populations (designated to a province by alphabetic code) are shown. ***A South Georgia****, A1 Falkland Islands, A2 South Shetland Islands, A3 South Orkney Islands, A4 South Sandwich Islands, A5 Gough Island, A6 Tristan da Cunha, A7 Bouvetøya, A8 Peter 1 Øy;* ***B Îles Kerguelen****, B1 Marion and Prince Edward Islands, B2 Îles Crozet, B3 Heard Island, B4 Amsterdam and St. Paul Islands****; C Macquarie Island,*** *C1 Auckland Islands, C2 Campbell Island, C3 Antipodes, C4 Bounty Island, C5 Chatham Island, C6 Balleny Islands;* ***D Peninsula Valdés***

Southern elephant seal distribution and status

South Georgia province. The island of South Georgia constitutes > 99% of the province's and *c.* 54% of the global population of southern elephant seals (approximately 397 000 individuals, Boyd *et al.* 1996). Smaller populations of elephant seals occur on the Falkland Islands, South Orkney Islands, King George Island, the South Sandwich Islands, Gough Island and Bouvet Island amongst others (Laws 1994). The South Georgia population has remained stable since 1951 (Boyd *et al.* 1996) but other island populations in this province may be in decline (e.g., Gough Island, Bester *et al.* 2001).

Kerguelen province. Numerically the second largest province, with principal elephant seal populations at Îles Kerguelen (153 200 individuals) and Heard Island (62 000 individuals), together with sub-populations at Îles Crozet (2000 individuals), Marion Island (1750 individuals) and Prince Edward Island (410) (Guinet *et al.* 1999, Slip and Burton 1999, Bester and Hofmeyr 2005, McMahon *et al.* 2005a, McMahon *et al.* 2009). All populations in this province appeared to have stabilized by the end of the 1990's (Guinet *et al.* 1999, McMahon *et al.* 2009) following substantial declines since the 1950's (van Aarde 1980, Bester *et al.* 1988, Bester and Lenglart 1982, McMahon *et al.* 2005a).

Macquarie province. In this province elephant seals breed on Macquarie Island (> 99%), Campbell Island and the Antipodes (McMahon *et al.* 2005a). Between 1952 and 2001, the Macquarie Island population declined from about 140 000 seals in the 1950's to a minimum of 64 000 individuals in 2001 (van den Hoff *et al.* 2007). Since then the population has increased slightly.

Peninsula Valdés. The increasing population at Peninsula Valdés is the only extant continental breeding population of southern elephant seals and numbers approximately 51 000 seals (Lewis *et al.* 2004).

Southern elephant seal biology

Southern elephant seals have a predictable annual haulout cycle characterized by well-defined pelagic phases at sea between distinct 'winter', moult and breeding haulouts on land (Le Boeuf & Laws 1994). The haulout cycle has been described for several populations (South Georgia, Boyd *et al.* 1996; Falkland Islands, Galimberti and Boitani 1999, Galimberti and Sanvito 2001; Heard Island, Slip and Burton 1999; Îles Crozet, Guinet *et al.* 1992; Marion Island, Kirkman *et al.* 2003, 2004; Macquarie Island, Hindell and Burton 1988; Peninsula Valdés, Lewis *et al.* 2004). The annual cycle of adult seals are often characterised by only two haulout phases: the breeding phase and the moult. Males haul out from August to mid-

September for the breeding phase and fight for status in a dominance hierarchy (McCann 1981). Elephant seals are extremely sexually dimorphic with adult males (1500 - 3000 kg) up to 10 times heavier than adult females (350 - 800 kg) (Le Boeuf and Laws 1994). The mating system is extreme polygyny (Fabiani *et al.* 2004) with females congregating in groups known as harems. Relatively small harems (<100 females) may be under the exclusive control of the highest ranking male (beachmaster) whereas larger harems are often controlled by a beachmaster and assistant-beachmaster(s), keeping subordinate bulls at the periphery of the harems. Elephant seals are extreme capital breeders (Boyd 2000) and females remain ashore for the entire lactation period of 21 to 23 days (Laws 1953, McCann 1980, Slip and Burton 1999). Numbers of females ashore during the breeding haulout (September to November) follow a reliable normal distribution (Hindell and Burton 1988) and can be used to estimate the total population size (Hindell and Burton 1987, McMahon *et al.* 2005b) by multiplying the number of females by a conversion factor (3.5, McCann 1985, Laws 1994; 3.15, Pistorius *et al.* 1999) estimated from the population age-structure. A few days after hauling out females typically give birth to a single pup weighing approximately 40kg at birth (but see McMahon and Hindell 2003). At Marion Island, pup mass averages 120kg (± 25kg SD) at weaning (McMahon *et al.* 2003).

The moult (November to March/April) is an obligatory haulout for all seals apart from the current season's weaned pups that moulted during the end of lactation or during the post-lactation period ashore. Seals moult sequentially according to age and breeding experience (Slip and Burton 1999, Kirkman *et al.* 2003). Site fidelity is lower during the moult compared to the breeding season (Nicholls 1970, Hofmeyr 2000) and some seals disperse to moult at non-native islands (e.g., Burton 1985, Bester 1988, 1989, van den Hoff 2001, van den Hoff *et al.* 2003). During autumn and winter, seals (mostly juveniles) may return to land for a facultative mid-year haulout (the purpose of which is still unclear). Participation in the mid-year haulout differs by age and sex (except among under-yearlings, Kirkman *et al.* 2001, Field *et al.* 2005) and although not correlated to future survival, participation in the winter haulout may increase (or be associated with) higher site fidelity (Pistorius *et al.* 2002).

Foraging and pelagic distribution

Southern elephant seals are wide-ranging marine predators and major consumers of cephalopods (squid) and fish (Green and Burton 1993, Santos *et al.* 2001, Daneri and Carlini 2002, Hindell *et al.* 2003). The global population has a circumpolar foraging distribution (Biuw

et al. 2007) and as a crude generalization, seals tend to migrate to high-latitude Antarctic waters or the Polar Frontal Zone during foraging trips (Bradshaw *et al.* 2003, 2004; Biuw *et al.* 2007). The physical oceanscape (e.g., sea temperature, salinity, sea-ice presence or absence, bathymetry, depth) encountered by seals during these extensive foraging migrations may vary markedly as seals traverse different frontal and oceanographic zones (Field *et al.* 2001, Hindell *et al.* 2003, Tosh 2010). Elephant seals dive continuously and deeply (up to 2000m but regularly to *c.* 400m) throughout their foraging trips (Hindell *et al.* 1991, Bailleul *et al.* 2007, McIntyre *et al.* 2010). Maternal investment, pup wean mass and juvenile survival, an important component in population dynamics, is influenced by prey availability and female foraging success (McMahon *et al.* 2000, 2003).

Southern elephant seals at Marion Island

The Marion Island southern elephant seal population is the only well-studied population within the southern Indian Ocean (Kerguelen province). This population, like all other southern Indian Ocean populations, declined by 87% from 1951 to 2004 (McMahon *et al.* 2009). In an attempt to understand the causal factors responsible for the decline and to quantify the life-history parameters for this small population, a comprehensive tagging study was commenced in 1983. The uninterrupted and ongoing mark-resight study (1983 to present) has since provided insight into many aspects of elephant seal biology, including life-history, demography, movements and philopatry (e.g., Pistorius *et al.* 1999, 2004, Hofmeyr 2000, Kirkman *et al.* 2003*,* 2004, McMahon *et al.* 2005b, de Bruyn 2009, Tosh 2010). The population experienced a change in growth rate in 1997 and is currently increasing (McMahon *et al.* 2009, Mammal Research Institute, unpublished data).

Objectives of this study

The marking and resighting of elephant seals form the cornerstone of all investigations into elephant seal biology at Marion Island. However, even though the tagging regime at Marion Island has extended more than an elephant seal generation (Hindell and Little 1988), a large proportion of seals hauling out here are unmarked (untagged). The occurrence of untagged seals at Marion Island is important as their presence suggests violation(s) of one (or more) of the assumptions of foremost mark-recapture analyses such as the Cormack-Jolly-Seber approach (Seber 1982, Lebreton *et al.* 1992).

The overall objective of this study was to:

1. investigate the origin of the untagged component of the southern elephant seal population at Marion Island, and

2. consider the demographic consequences of the untagged component for the mark-resight experiment and population as a whole.

Specifically, these objectives were addressed in four sections:

1. To describe the composition of the southern elephant seal population that haul out at Marion Island to breed, moult and winter in terms of numbers of tagged and untagged seals.
   a. Do untagged seals have variable relative abundance during different haulout phases?
   b. Is the relative abundance of untagged seals related to age class?
   c. Is there a trend in the relative abundance of untagged seals over years?
   d. How do untagged seals distribute spatially relative to tagged seals?
   e. Do the observed patterns elucidate the possible origin of this untagged population component at Marion Island?

2. To calculate the rate of flipper tag-loss for southern elephant seals marked at Marion Island in the ongoing mark-resight study.
   a. What are the age and sex specific tag-loss rates?
   b. Do different tagging personnel have an effect on tag-loss?
   c. Does tag site (location of tag on flipper) affect tag-loss rates?

3. To investigate local intra-archipelago movement (dispersal and dispersion) of southern elephant seals at the Prince Edward Islands.
   a. To what extent are intra-archipelago movements of elephant seals in the PEI group occurring?
   b. Are the resighting histories of Marion Island-tagged seals observed at Prince Edward Island typical for individuals of the Marion Island population?
   c. What is the significance of the findings for the ongoing mark-resight programme at Marion Island?

4. To investigate movement of southern elephant seals within the Kerguelen province, with special interest in dispersal and dispersion rates between Marion Island and other populations in this province.

   a. To what extent are dispersal and/or dispersion occurring?

   b. Can dispersal be described as natal- or breeding dispersal and is gene flow occurring (i.e., do dispersing individuals reproduce)?

   c. Are dispersal and/or dispersion associated with specific sex or age classes?

   d. Are foreign seals transient visitors to Marion Island (occur only once) rather than potential immigrants to the population (repeatedly sighted)?

   e. What is the potential impact of immigration on the growth rate of the Marion Island elephant seal population?

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CHAPTER 2

STUDY AREA

Southern Ocean

The Southern Ocean is one of the largest and most productive marine ecosystems on earth, constituting *c.*10% of the global ocean environment (Constable *et al.* 2003). In contrast to the northern hemisphere, where land occupies half the area between 30°N and 60°N, the circumpolar Southern Ocean overshadows land area by 16:1 between latitudes 30°S and 60°S (Chown *et al.* 2004). Extending northwards from the Antarctic continent, it is the most prominent and dominant physical force in this latitudinal band of the southern hemisphere. Sparsely distributed Southern Ocean or sub-Antarctic Islands are of considerable biological and conservation importance (Chown *et al.* 1998) despite their comparatively insignificant size to the total area of the region.

The distribution of resources within the Southern Ocean is unpredictable and heterogeneously distributed in space and time (Guinet *et al.* 2001, Constable *et al.* 2003) and depends on the physical oceanographic features such as bathymetry, circulation patterns and hydrographic processes (Lutjeharms *et al.* 1985, Tynan 1998, Knox 2007). Fundamental to the distribution of resources is the circulation of Antarctic water from the continental shelf to a latitude of around 40°S (Knox 2007). The main driving force for Southern Ocean circulation is wind; in particular the prevailing westerly winds within a circumpolar belt from 40°S to 50°S, known as the "roaring forties". The Antarctic Circumpolar Current (ACC), the strongest and one of the widest world ocean currents (Tynan 1998) is associated with the maximum wind field within these latitudes. The westerly wind results in the predominantly east flowing water of the current (Knox 2007). The Prince Edward Islands lie directly in the path of the ACC in a region known as the Antarctic Polar Frontal Zone (PFZ), between the Antarctic Polar Front (APF) in the south, and the sub-Antarctic Front (SAF) to the north (Lutjeharms and Valentine 1984). The exact location of the fronts is variable, however, and show considerable inter-annual meridional shifts in latitude (Lutjeharms and Valentine 1984).

The Prince Edward Islands in the Southern Ocean

The Prince Edward Islands (PEIs) comprises two islands, Marion Island and Prince Edward Island, in the sub-Antarctic region of the Southern Ocean. The islands are volcanic outcrops,

Marion Island at least half a million years old (McDougal *et al.* 2001). The archipelago pinnacle rises steeply from the complex bottom topography (Ansorge and Lutjeharms 2002), especially to the south of the island where it rises from about 5000m depth (Lutjeharms and Ansorge 2008). A shallow saddle, 40 to 200m deep separates the two islands (Ansorge and Lutjeharms 2002). The PEIs constitute an isolated surface feature within the Southern Ocean, with Île aux Cochons, of the Îles Crozet archipelago 950 km to the east, being the nearest landfall. Îles Crozet is situated on the easternmost extremity of the Crozet Plateau, a large shallow rise (often <2000m) that extends from the northeast of PEIs to Îles Crozet (Lutjeharms and Ansorge 2008).

The terrestrial and oceanic environment of the PEIs region is strongly influenced by the ACC (Lutjeharms and Ansorge 2008). Although predominantly east flowing, bottom topography deflects much of the current upstream of the PEIs. The South-West Indian Ridge (SWIR), extending from the south-west to the north east, lies directly west of the PEIs. The SWIR, and in particular the Andrew Bain fracture zone, plays an important role in creating extreme mesoscale variability ("a turbulent environment") characterized by enhanced primary productivity (Pollard and Read 2001, Lutjeharms and Ansorge 2008). Mesoscale variability, effectively a range of eddies, are generated in this area (SWIR) (Ansorge and Lutjeharms 2003) and these eddies constitute important foraging areas for pelagic predators as they move towards the PEIs. Areas of higher primary productivity also occur at the frontal systems (APF and SAF) and pelagic predators also concentrate feeding at these fronts (Lutjeharms and Ansorge 2008).

The Prince Edward Islands terrestrial environment

The PEIs provide a breeding and moulting site for large populations of seabirds and seals (Ryan and Bester 2008). Marion Island is the larger of the two islands (projected surface area 290 km², actual surface area [i.e. taking slopes into account] 300 km²; Prince Edward Island 46 km², Meiklejohn and Smith 2008) and rises to 1240m above sea level. The islands have rugged coastlines characterised by coastal cliffs, narrow rockfall shores and intermittent boulder beaches of varying size. Elephant seals prefer to haul out on beaches with even profiles and a sand, pebble or rounded boulder (diameter <0.5m) substrate (Condy 1978). Only three sites have sandy substrates (two beaches on Marion Island and one on Prince Edward Island). Suitable haulout beaches are separated from each other by stretches of

coastline inaccessible or unfavoured by elephant seals, leading to well defined haulout sites of mostly boulder or pebble substrate (Wilkinson *et al.* 1987) (Figure 2.1).

Figure 2.1. Southern elephant seal females and pups on a breeding beach on the east coast of Marion Island. Suitable haulout beaches are separated from each other by stretches inaccessible coastline. Photo: R.R. Reisinger.

The vast majority of haulout sites favoured by elephant seals occur on the northern and eastern (leeward) side of the PEIs, although two haulout sites on the southern coast of Marion Island are of importance. The majority (*c.* 60%) of beaches occur at drainage lines and are often small (<100m long). Some suitable boulder beaches lie at the base of coastal cliffs. Although often longer than drainage line beaches, cliff-base beaches are usually narrow with coastal cliffs preventing seal movement to the coastal plains (Condy 1978). The local spatial distribution of elephant seals varies depending on the haulout type (Mulaudzi *et al.* 2008). During the breeding season seals aggregate in harems on some of the beaches, however,

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during the moulting season many seals haul out on drainage line beaches and then move to the coastal plain to moult and wallow (Condy 1978). Here they modify the immediate environment by creating hollows that disrupt local drainage and change vegetation (Panagis 1984).

The windward southern and western coastlines of the PEIs are exposed to powerful wave action and is characterised by narrow rugged boulder and rockfall beaches backed by high, sloping cliffs. Fur seals (*Arctocephalus tropicalis* and *A. gazella*) occupy these beaches; however, they are seldom used by elephant seals (Condy 1978). Although some elephant seals are usually encountered during the moult, breeding is especially rare from the Rooks Peninsula in the south, clockwise to Storm Petrel Bay in the north on Marion Island (Mammal Research Institute, unpublished data) (Figure 2.2).
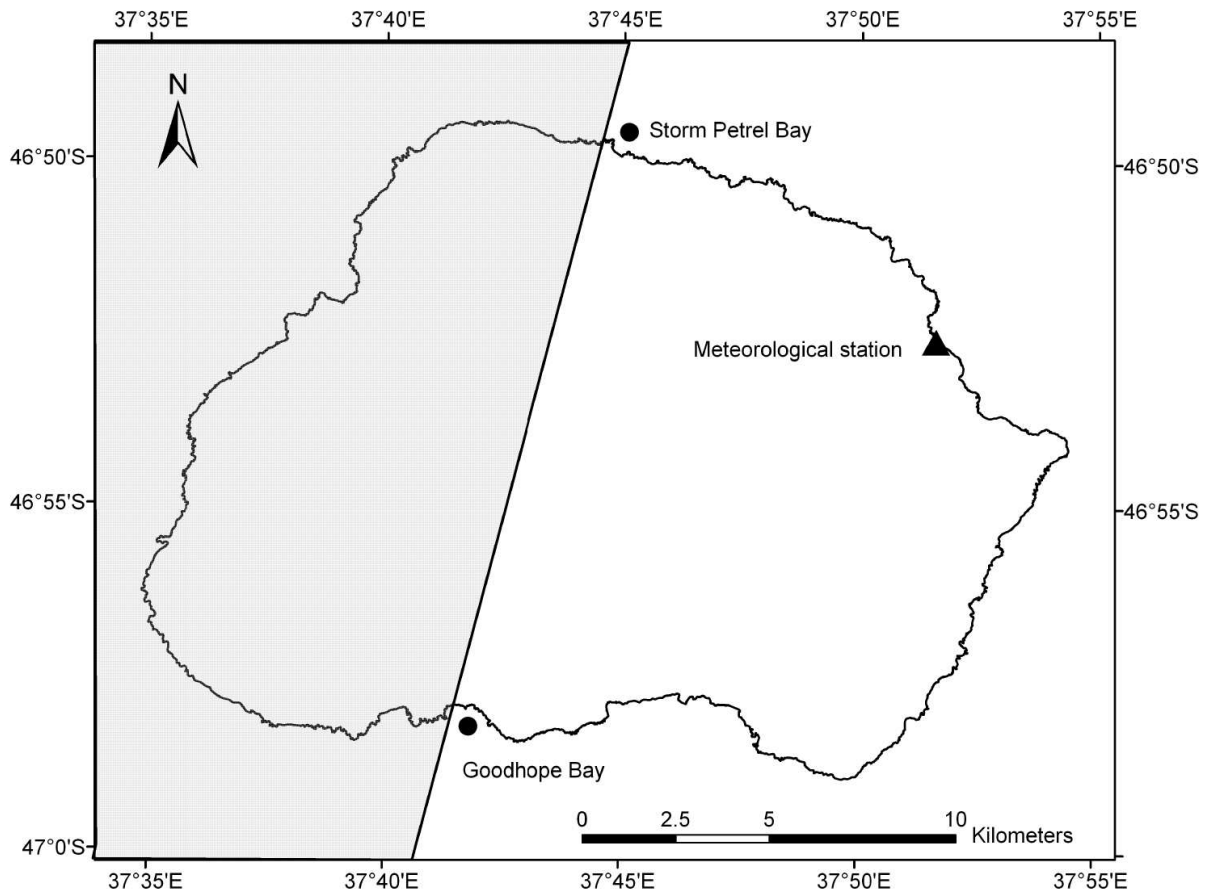

Figure 2.2. Marion Island. The main study area is from Storm Petrel Bay in the north, clockwise to Goodhope Bay in the south.

Climate and climate change

The remoteness of the PEIs in the extensive Southern Ocean results in a hyper-oceanic or hyper-maritime climate (Boelhouwers *et al.* 2003). The local climate is modified by a continued progression of mid-latitude depressions (*c.* 100 per year, Smith 2002), frontal systems and migratory anticyclones in the region of the islands (Rouault *et al.* 2005). Low air temperatures which differ little from the sea surface temperature occur throughout the year, with minimal daily and seasonal temperature fluctuations (Smith and Steenkamp 1990). Annual temperatures averaged 6.4°C and annual precipitatio n (rain, snow, ice and mist) averaged *c.* 2000mm in the 1990s (Smith 2002, le Roux and McGeoch 2008). The prevailing wind direction is from the west (average wind speed >10m.s^{-1}) and wind exposure is a prominent force shaping the distribution of terrestrial vegetation types on the islands (Smith and Steenkamp 1990).

Climate change has resulted in rapid warming and drying of the PEIs (le Roux and McGeoch 2008). Sea surface temperatures increased by 1.4C from 1949 - 1999, which translates to twice the mean global rate (Mélice *et al.* 2003). Climate change is expected to impact on oceanographic circulation, and the position and intensity of major frontal systems within the PEIs region of the Southern Ocean (McQuaid and Froneman 2008). Since the 1970's, a one degree southward shift (amid large inter-annual variation) in the average meridional position of the SAF has been observed (Hunt *et al.* 2001). A southward migrating SAF will increase the frequency of influx of warmer sub-Antarctic water to the APF. This would effect a modification of the food chain through changes in the zooplankton community, together with a decrease in the total zooplankton biomass production due to the influx of low productivity sub-Antarctic surface water (Hunt *et al.* 2001, Bernard and Froneman 2003). Changes in the zooplankton community are expected to have ramifications for the pelagic predators higher up in the food chain through changes in food availability. The immediate consequences of such an ecosystem change for pelagic predators are expected to vary depending on the foraging strategies of the predators (McQuaid and Froneman 2008).

Conservation Status

The PEIs, governed under the sovereignty of South Africa, were proclaimed a Special Nature Reserve in 1995, in terms of the Environmental Conservation Act (Act 73 of 1989). This Act requisites areas to be managed mainly for science or wilderness protection, and necessitates a management committee and management plan to regulate all activities at the site (Hänel

and Chown 1998, de Villiers and Cooper 2008). The current management authority of the PEIs is the Department of Environmental Affairs' Directorate: Antarctica and Islands. The Prince Edward Islands Management Committee provides advice to the Directorate in accordance with The Prince Edward Islands Management Plan (PEIMPWG 1996). A revised management plan (Chown *et al.* 2006) depicts the current conservation strategy for the islands.

On Marion Island, management zones restrict access to areas sensitive to human interference (Hänel and Chown 1998). Prince Edward Island is regarded as one of the most pristine Southern Ocean Islands (de Villiers and Cooper 2008) and is a Protected Zone, with a limit of one visit every two years by a maximum of 10 persons for 8 days (Chown *et al.* 2006). Restricted access to the PEIs and Prince Edward Island in particular aims to prevent the introductions of new alien species to the islands, where previous introductions threaten biodiversity (Chown *et al.* 1998). This preventative measure largely confines long-term intensive scientific research to Marion Island.

An exclusion zone prohibits fishing within 12 nautical miles of the PEIs (Marine Living Resources Act of 1998, de Villiers and Cooper 2008). In addition, a Marine Protected Area (MPA) is considered, to expand the protected marine area to include some of the 200 nautical mile Exclusive Economic Zone (EEZ) around the PEIs (Lombard *et al.* 2007). South Africa is a member of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). One of the objectives of CCAMLR is to maintain ecological relationships and to prevent irreversible ecosystem changes (Agnew 1997). A summary of the protection offered to the PEIs through national legislation and international agreements appears in de Villiers and Cooper (2008).

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CHAPTER 3

RELATIVE ABUNDANCE AND HAULOUT PATTERNS OF UNTAGGED

SOUTHERN ELEPHANT SEALS AT MARION ISLAND

W.C. Oosthuizen *et al.*

Abstract

At Marion Island, southern Indian Ocean, virtually all southern elephant seal *Mirounga leonina* pups born annually (1983 - 2008) were marked with durable hind flipper tags in a long-term mark-resight study. However, large numbers of untagged seals, either migrants from other islands or previously tagged seals which suffered tag-loss, haul out at this locality. We fitted a generalized linear model to assess the significance of month, year and age class on the relative abundance of untagged seals from 1997 to 2009 and determined the variation in spatial onshore distribution of untagged seals relative to tagged seals using a binomial test. The relative abundance of untagged seals fluctuated according to the annual haulout cycle. Untagged seals, predominantly juveniles, were present in the highest proportion (> 70%) during the winter haulout and the lowest (but still substantial) proportion (*c.* 50%) during the female breeding haulout. Proportionally, adult females had the least number of untagged seals, the greatest number of untagged seals present in juvenile age categories. Untagged seals increased in relative abundance from 1997 to 2009. Untagged seals distributed evenly around suitable haulout beaches at Marion Island while tagged seals display high local site fidelity and occur in greater numbers on the northeastern coastline. Untagged seals are considered to be mostly migrant seals that disperse from other islands within the southern Indian Ocean and haul out at Marion Island during non-breeding haulouts in particular, from which a proportion will immigrate into the breeding population. Overall, the haulout patterns of untagged seals do not fit the tag-loss hypothesis as the principal source of untagged seals at Marion Island.

Keywords: dispersal, distribution, haulout, long-term, Marion Island, mark-resight, *Mirounga leonina*, population count, unmarked

Introduction

Effective conservation or management of wildlife populations is, in part, dependent on reliable long-term knowledge of the life history parameters that influence population regulation. Often, the parameters of interest are survival and fecundity of individuals or groups (representing fitness), and how these vital rates change through time and space (Lebreton *et al.* 1992). Individually based, long-term, longitudinal mark-recapture studies are ideal to identify the most important processes affecting the population dynamics of the component species, including processes that would not be obvious from shorter studies (e.g., Coulson *et al.* 1997, Coltman *et al.* 2002). Additionally, long-term time series abundance data are required to assess the importance of intrinsic and extrinsic factors driving population trends of long-lived species (Weimerskirch *et al.* 2003, McMahon *et al.* 2005a, 2009).

The southern elephant seal *Mirounga leonina* is an abundant, wide-ranging marine predator with a circumpolar Southern Ocean distribution (Figure 3.1, McMahon *et al.* 2005a). Southern elephant seals have a predictable annual haulout cycle characterized by well defined pelagic phases at sea between distinct 'winter', moult and breeding haulouts on land (Le Boeuf & Laws 1994). Populations of southern elephant seals in the southern Indian Ocean (Kerguelen, Heard, Crozet, Marion and Prince Edward islands) and southern Pacific Ocean (Macquarie Island) declined by as much as 80% from 1950 to 2000 (McMahon *et al.* 2005a). In an attempt to understand the causal factors responsible for the decline at Marion Island (87% decline from 1951 to 2004, McMahon *et al.* 2009), a long-term demographic study was established in 1983 to quantify the life-history parameters for this small, and at the time, declining population. The uninterrupted and ongoing mark-resight study (1983 to present) has since provided insight into the life-history, demography, movements and philopatry of southern elephant seals at this locality (e.g., Pistorius *et al.* 1999, 2004, Hofmeyr 2000, Kirkman *et al.* 2003, 2004, McMahon *et al.* 2005b, de Bruyn 2009, Tosh 2010). The small population size (~ 500 breeding females) permits marking of all pups born at the island (by flipper-tagging, see de Bruyn *et al.* 2008), while the predictable haulout cycle (Kirkman *et al.* 2003, 2004) and high site-fidelity (Hofmeyr 2000) allow for an intensive resight schedule with high encounter (resight) rates (McMahon *et al.* 2003). However, even though the tagging regime at Marion Island has extended more than an elephant seal generation, a large proportion of seals hauling out here are unmarked (untagged). The occurrence of untagged seals at Marion Island is important as their presence suggests violation(s) of one (or more) of the basic assumptions (no dispersal

and no marker loss [Pollock 2000]) of foremost mark-recapture analyses such as the Cormack-Jolly-Seber approach (Seber 1982, Lebreton *et al.* 1992).

Untagged seals observed at Marion Island may come from three sources. Firstly, a proportion of pups born at Marion Island may escape tagging at weaning, violating the assumption that the total population is marked every year. The number of pups that escape tagging can be estimated by comparing the actual number of pups tagged to the expected number of pups weaned at a specific site, based on the number of females resighted at this site during the course of the breeding haulout and subtracting cases of pre-weaning mortality. This assumption is valid as, for example, from 2003 to 2008, 2425 recently weaned pups were tagged on Marion Island while only 11 to 19 pups (0.45 - 0.78%) escaped tagging. Although the number of pups that escaped tagging may have been somewhat higher in the initial period of this study (1983 - 1989), very few pups born in subsequent cohorts depart from Marion Island without being double tagged and therefore we reject this hypothesis as a source of untagged seals from the onset.

Alternatively, tagged Marion Island seals may lose both flipper-tags over time and survive as untagged seals, indistinguishable from seals never tagged. Although estimated tag-loss rates are modest for this research programme (Pistorius *et al.* 2000, Oosthuizen *et al.* 2010), tag-loss dependence (tags on the same animal are not lost independently, McMahon and White 2009) would underestimate the number of seals that lose both tags. If tag-loss is the foremost source of untagged seals at Marion Island, we expect juvenile (under-yearling, yearling, subadult) age classes to have the greatest proportion of tagged individuals, with a decline in the number of tagged individuals relative to untagged individuals as seals age. Finally, untagged seals observed at Marion Island may be migrants (non-breeding) or immigrants (part of the breeding population), having dispersed from other elephant seal populations within the southern Indian Ocean, or even further afield. Such movement is predicted to be migratory, involving mostly immature seals (Bester 1989).

This chapter describes the composition of the southern elephant seal population in terms of tagged and untagged seals that haul out at Marion Island to breed, moult and winter. Age class, and temporal and spatial distributions of untagged seals relative to the numbers of tagged seals are given. The possible origin of this untagged population component at Marion Island and consequences for the ongoing mark-resight study are discussed.

Methods

Study area

The Prince Edward Islands (PEIs) comprise two islands, Marion Island (300 km²) and Prince Edward Island (46 km^2; 19 km to the northeast of Marion Island), in the sub-Antarctic region of the southern Indian Ocean (Figure 3.1). The PEIs constitute an isolated surface feature north of the Antarctic Polar Front (APF), with Île aux Cochons of the Îles Crozet archipelago, 950 km to the east, being the nearest landfall. Îles Kerguelen (2640 km) and Heard Island (2740 km), where the largest populations of southern elephant seals within this sector of the Southern Ocean occur (Guinet *et al.* 1999, Slip *et al.* 1999), are located on or just south of the APF further to the east.

Field methods

Since 1983, virtually all recently weaned southern elephant seal pups born at Marion Island were sexed and double tagged in the interdigital webbing of the hind flippers with identical, uniquely numbered, colour-coded plastic Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom) (de Bruyn *et al.* 2008). In conjunction with double tagging, a high and near constant resighting effort including all beaches along a 51.9 km coastline where southern elephant seals regularly haul out was implemented (from Storm Petrel Bay in the north, clockwise to Goodhope Bay in the south, see Figure 3.1). All haulout sites around the island are identified by numerical codes (MM001 - MM068). For brevity, these are given as 01 to 68 in this manuscript. During the moulting and winter periods (mid-November - mid-August), one or two observers searched all beaches for tagged seals every ten days, but in the breeding season (mid-August - mid-November) beaches were searched by two observers on a seven-day cycle to allow for increased seal numbers and harem density. Beaches on the west coast where elephant seals infrequently haul out were visited once a month. For every tagged seal resighted, the date, locality, tag colour combination and three-digit number, number of tags remaining, and the sex of the seal (if identified) were recorded. Untagged seals were counted and grouped into age class categories (under-yearling [< 1 year], yearling [1 to < 2 year], subadult [2 to < 3 {females}; 2 to < 5 {males}], adult female [>3 {if breeding}], adult male [>6 year]) based on visual comparison to known aged seals.
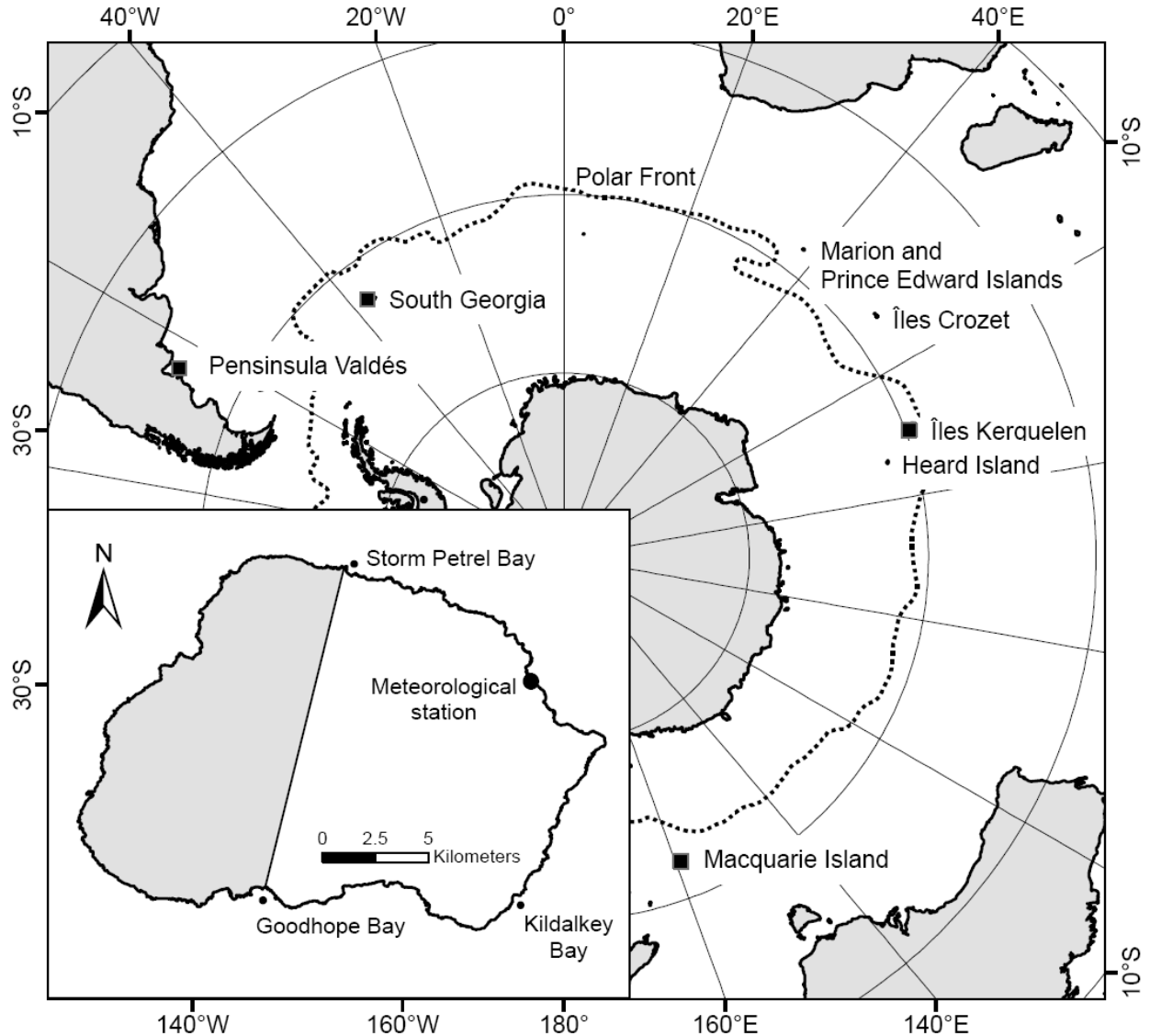
Figure 3.1. The distribution of the major breeding populations of southern elephant seal in the Southern Ocean (squares) and the location of elephant seal sub-populations within the southern Indian Ocean. Inset: Marion Island. The main study area (see above) is from Storm Petrel Bay in the north, clockwise to Goodhope Bay in the south.

The total number of seals present on every beach during regular censuses was recorded from April 1990 to April 1997. For this period, the total number of tagged seals observed could be estimated from the individual tag-resight database; however, these may include tag-resights that were made on secondary or opportunistic occasions, additional to the regular censuses. From May 1997 to April 2009, more comprehensive "site-census data" were recorded at every

beach (site) where elephant seals were observed during regular censuses. Site-census data comprise of the number of seals recorded in each age class, the number of these seals inspected for the presence of tags and the number of seals bearing "Marion Island" tags.

Analyses

Although it is possible to determine the absolute number of individual untagged seals present at Marion Island during any single census, the fact that they are untagged (i.e. unidentifiable) precludes exact calculation of seasonal or annual numbers of individuals. Furthermore, seal numbers fluctuate seasonally according to the haulout cycle. Therefore, to determine the relative abundance of the untagged population component, we compared the number of untagged seals relative to the number of Marion Island tagged seals. This estimate, defined as the "tag-ratio", is expressed as the proportion of tagged individuals (the number of tagged seals present divided by the number of seals inspected for tags). Seals not inspected for tags on any particular occasion were excluded from analyses (*c.* 5% of seals encountered on any particular census; Mammal Research Institute, unpublished data).

Temporal variation in tag-ratios was considered at monthly and annual time scales. Monthly comparisons allow detailed partitioning of the annual haulout cycle which in brief, involves the synchronous breeding season (August to November [adult males], September to November [adult females], Kirkman *et al.* 2004), obligatory moult (November to March/April, Kirkman *et al.* 2003) and autumn/winter mid-year haulout in which juvenile seals predominate (Kirkman *et al.* 2001, Field *et al.* 2005). Annual comparisons (n = 11) were made between "expedition years", from beginning May$_{(t)}$ to end April$_{(t+1)}$. Site-census data were not reliably collected from May 2002 to April 2003 and were excluded from all analyses. Additionally, the entire adult female and partial adult male (not breeding season records) components of 2001 and the entire adult male component of 2004 were excluded due to incongruous data collection for these age classes in the specific years. Site-census data were grouped into five age class categories: adult males, adult females and mixed-sex groups for subadults, yearlings and under-yearlings. We initially fitted a generalized linear model (GLM, McCullagh and Nelder 1989) with binomial error distribution and a logit link function (Venables and Ripley 2002) using programme R (R Development Core Team 2004), with year, month, age class and all second order interactions as explanatory variables. In binomial GLMs, the deviance is chi-squared distributed with the residual deviance expected to be approximately equal to the residual degrees of freedom. As we found evidence of overdispersion in initial modeling using

the binomial family argument (residual deviance greater than residual degrees of freedom, dispersion parameter = 3.04), we refitted the model using quasi-likelihood (family = quasibinomial) that need not correspond to any particular distribution (Venables and Ripley 2002). The significance of terms in the model was assessed using F tests (analyses of deviance) with significance level set as $p < 0.05$ (Hardy 2002, Crawley 2007).

The spatial distribution of tagged seals relative to that of untagged seals was compared for sites ($n = 43$) where in total, more than 100 seals were inspected for tags between May 1997 and April 2009. During this period, the overall mean tag-ratio at all sites was 0.378 (48 555 tagged seals from 128 302 seals inspected). To examine whether certain sites had higher proportions of tagged individuals than expected, we applied a two-tailed binomial test (binom.test) in R with the hypothesized probability of success (p) set to 0.378. This model tests the null-hypothesis that p = 0.378 and the alternative that p ≠ 0.378 for every site. We used the 95% confidence interval (CI) for the probability of success to categorize sites as having lower than expected tag-ratios (upper 95% CI below 0.378) or higher than expected tag-ratios (lower 95% CI above 0.378). Sites where the 95% CI contains 0.378 exhibit no evidence to reject the null hypothesis. Correspondingly, the total number of seals observed at each site during the study period and the age class specific utilization of a site were used to elucidate differences in tag-ratios between sites.

Results

GLM model

Counts of seals (marked and unmarked combined) fluctuated predictably throughout the study period as a function of the cyclic haulout pattern of elephant seals. Seal numbers increased during the breeding season (~ October), followed by a peak in numbers during the annual moult (~ December, Figure 3.2). A smaller, secondary peak occurred during April to May (autumn/winter haulout).
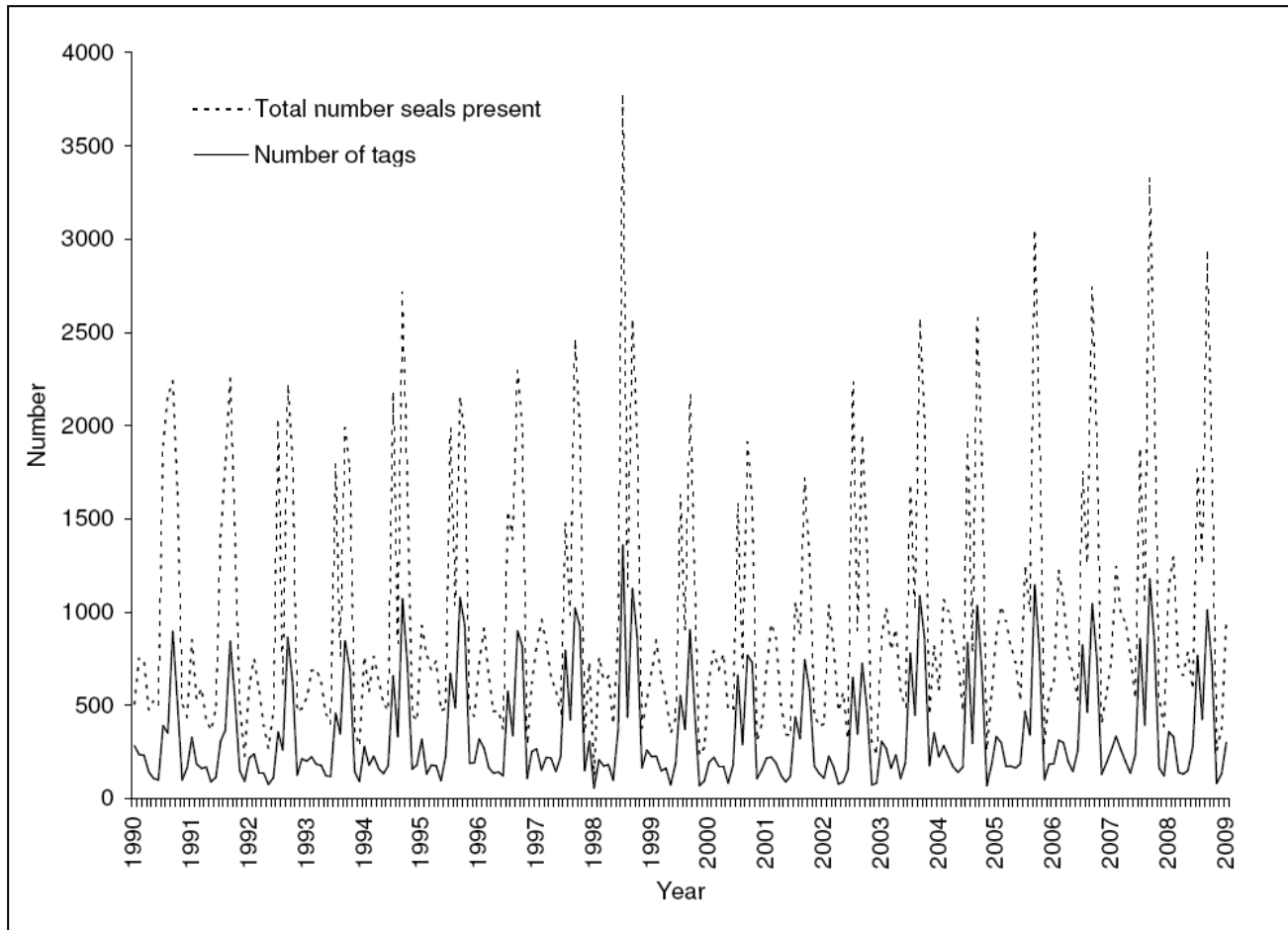
Figure 3.2. Time series data of southern elephant seal resights at Marion Island. The y-axis corresponds to the total number of seals recorded during regular censuses (dotted line) and the number of tagged seals observed (solid line). Multiple resights of the same individual during a single haulout period are included. Higher numbers in October 1998 are due to an increase in observer effort along a section of the study area coastline (counts conducted on alternate days, see Kirkman et al. 2004 for details), rather than an increase in seals.

All first and second order terms included in the starting GLM model were highly significant ($p <$ 0.001). Monthly differences in tag-ratios ($F = 31.80$, $df = 11$, $p < 0.001$) largely correlated to seasonal or haulout patterns (Figure 3.3). The greatest proportion of tagged animals was present during the breeding season (September and October) with a maximum tag-ratio during the peak adult female haulout in October when on average, 50% of the population in attendance have tags. In the last three years of the study, this proportion is derived from approximately 520 (tagged and untagged combined) breeding females per annum. Tag-ratios declined after the breeding season (November) amid the onset of moult, which lasts to

January/early February (adult females) or March (adult males). Tag-ratios during the peak moult ranged from 0.40 (mean value, November) to 0.43 (January). Proportionally, the fewest tagged individuals (lowest tag-ratio) hauled out during the austral autumn and winter (April to August) and tag-ratios reached a minimum (mean = 0.22) in August, immediately prior to the onset of the breeding season. Monthly tag-ratios varied somewhat between years (Figure 3.3, $F = 1.69$, df = 110, $p < 0.001$), but this variation did not obscure the seasonal pattern in tag-ratios according to the haulout cycle.

Age class had a strong influence on tag-ratios ($F = 218.40$, df = 4, $p < 0.001$). Adult males (0.43) and adult females in particular (0.49), recorded the greatest proportions of tagged seals relative to the number of untagged seals; yet these ratios were still below 0.5, indicating that more than half of all adult seals resighted were untagged. Juvenile age categories had lower tag-ratios which decline with age (Figure 3.4). On average, subadults and yearlings encountered had a 0.36 and 0.32 probability of carrying tags respectively, while under-yearlings (0.26) had the lowest probability of carrying tags. Tag-ratio probabilities varied for age classes within a year depending on the haulout phase (delineated by month; age:month interaction $F = 11.58$, df = 44, $p < 0.001$).
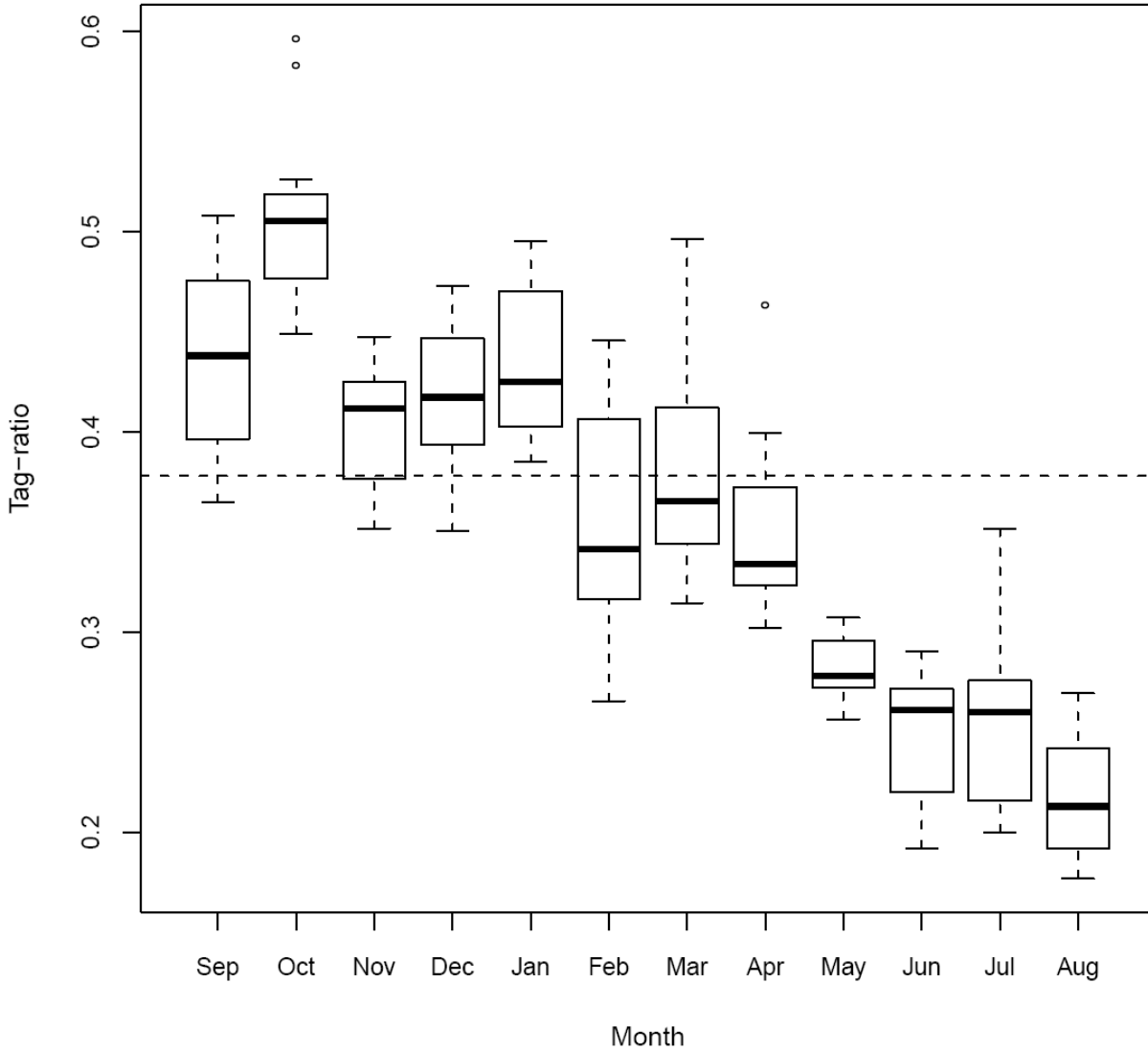
Figure 3.3. Monthly fluctuation in tag-ratios (proportion of tagged individuals). For the purpose of this figure, a year begins in September (the start of the female breeding haulout) and ends in August. The horizontal line at 0.378 indicates the overall mean annual tag-ratio. Horizontal boxplot lines show the median tag-ratio for each month and boxes represent the 25th and 75th percentiles, respectively. The vertical dashed lines show either the maximum value or 1.5 times the interquartile range of the data (whichever is the smaller). Outliers are plotted individually. Data was collected monthly from May 1997 to April 2009, excluding 2002 (n = 11).
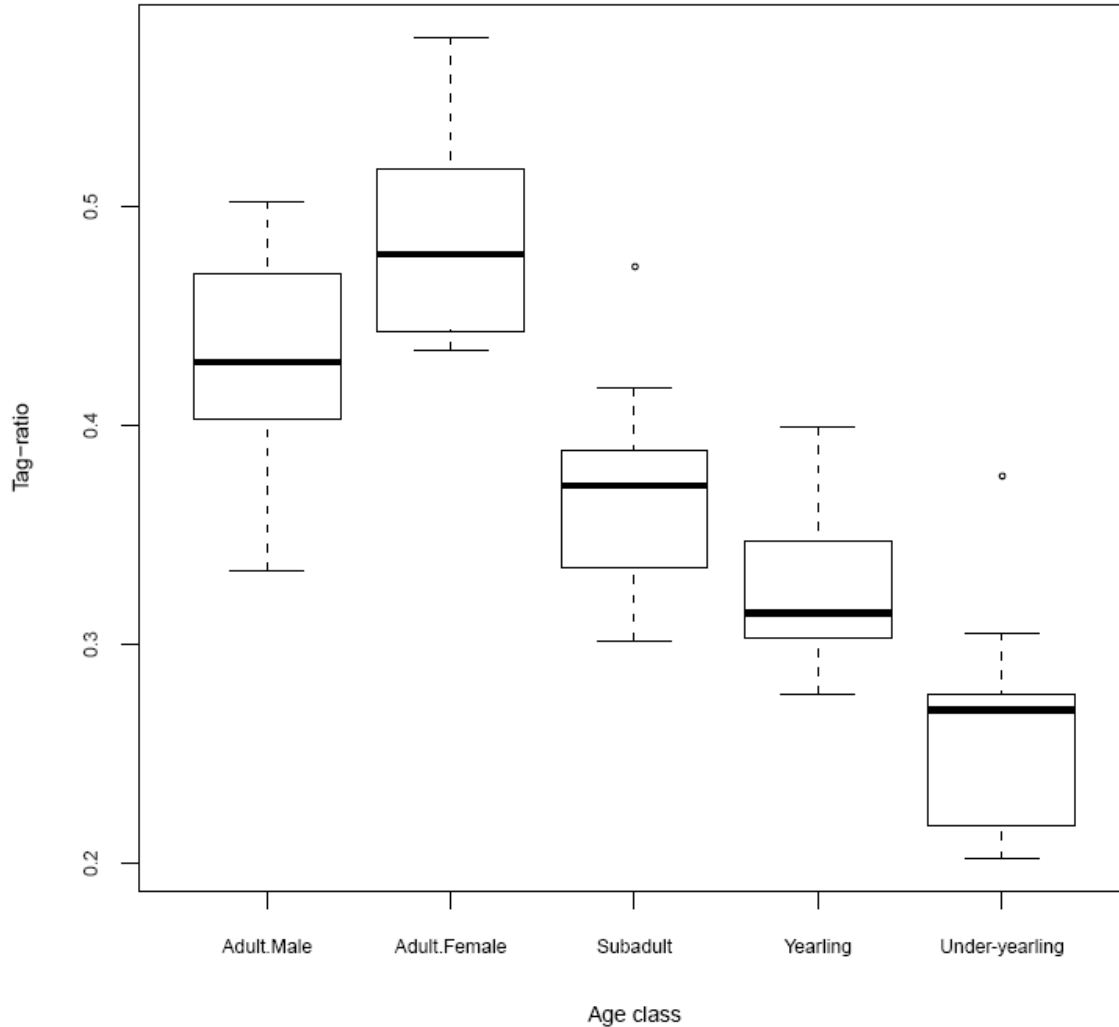
Figure 3.4. The distribution of tag-ratios (proportion of tagged individuals) in relation to age class. All haulout phases are considered.

Tag-ratios declined from 1997 to 2009 (F = 14.04, df = 10, p < 0.001) and model fit was improved by separating the response of different age classes (F = 3.50, df = 38, p < 0.001). Adult male tag-ratios varied more than other age classes between years (SD = 0.54, mean SD for other age classes = 0.45), and did not appear to decline systematically (-0.0029 year^{-1}). The slope of the regression line of the fitted probabilities predicted by the GLM was negative for all other groups: adult females (-0.0064), subadults (-0.0063), yearlings (-0.047) and under-yearlings (-0.0065) (Figure 3.5).
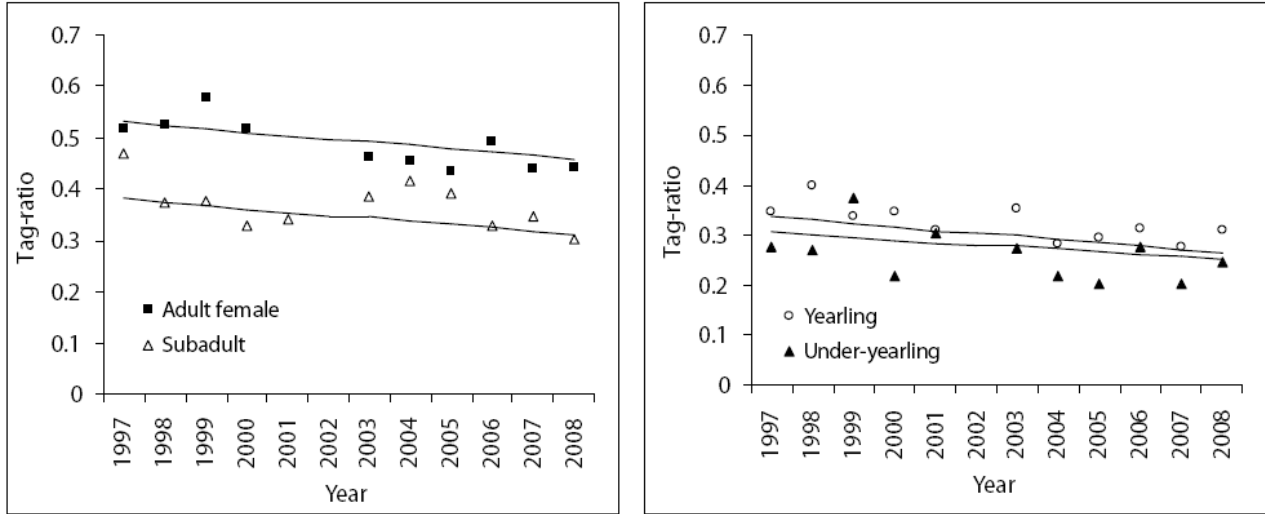
Figure 3.5. Southern elephant seal tag-ratios (proportion of individuals tagged) at Marion Island from May 1997 to April 2009 (excluding 2002, n = 11). Mean observed proportions (points) and fitted probabilities (lines, GLM model) for different age groups are shown.

Spatial analyses

Sites on the north-eastern aspect of Marion Island (n = 12), from Goney Bay in the north (53) to Ship's Cove in the south (65) had higher proportions of tagged seals than expected (Figure 3.6). Three other locations on the island's southern aspect, namely Funk Bay (18), Kildalkey Bay (20) and Goodhope Bay (26), had higher than expected tag-ratios, where the 95% CI for the probability success did not include 0.378 (see Methods). Sites with lower than expected tag-ratios (n = 16) and those with tag-ratios similar to the mean (n = 12) were interspersed along the east coast (Figure 3.6).

The total number of seals that occupied a specific site over time did not explain the spatial variation in tag-ratios (linear model, p = 0.40, R^2 = 0.017, Figure 3.7a), although on average, sites with lower than expected tag-ratios had fewer seals (2227 ± 2519 seals, mean ± SD, 28 sites) than sites with 95% CI above 0.378 (4067 ± 2845 seals, mean ± SD, 15 sites). More importantly, age class specific utilization of different sites influenced spatial variation in tag-ratios. Sites with higher tag-ratios (> 0.378) had greater proportions of adult seals utilizing the site relative to juvenile seals, while sites with tag-ratios below 0.378 were utilized by greater proportions of juvenile seals (Figure 3.7b).
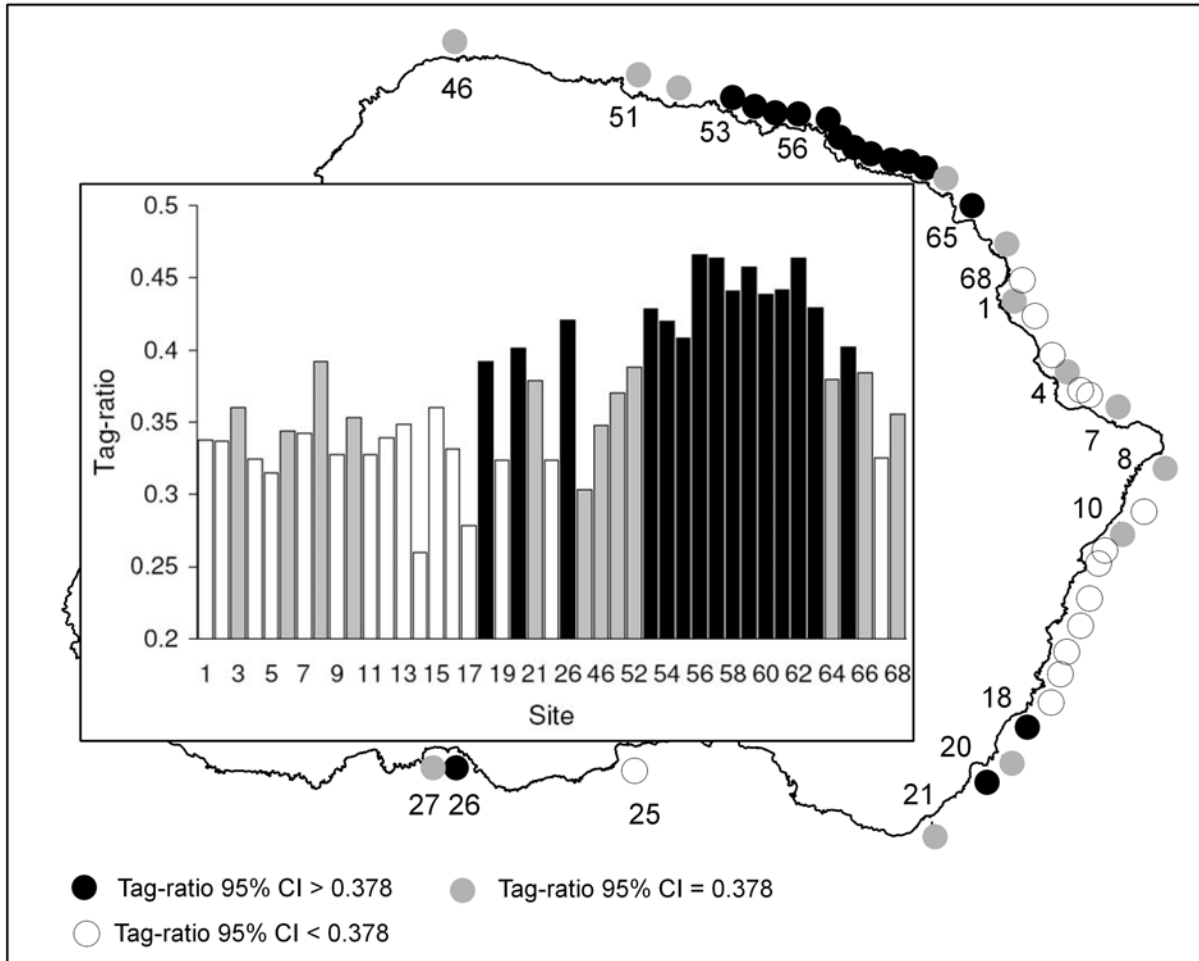
Figure 3.6. Spatial variation in tag-ratio for all beaches (sites) where more than 100 elephant seals were recorded during all seasons from 1997 - 2009. The map shows the location of sites with codes corresponding to the "Site" axis in the histogram.
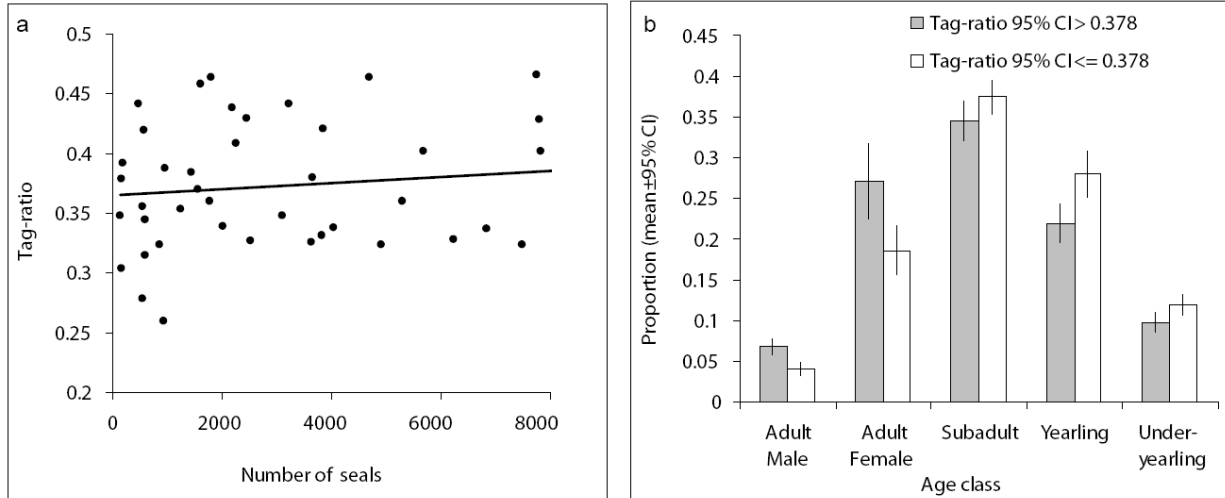
Figure 3.7. a. The total number of seals that utilizes a site does not significantly influence the tag-ratio (proportion of tagged individuals) recorded for that site. b. The proportion of seals recorded per age class (relative use of a site by each age class) for sites with tag-ratios above and below 0.378 respectively. Sites with tag-ratios above 0.378 have a higher proportion of adult seals and less juvenile seals that utilize the site, as compared to sites with tag-ratios below 0.378.

Discussion

Nearly all southern elephant seal pups born on Marion Island are tagged annually, in contrast to elephant seal mark-resight studies at locations with large populations where only a proportion of the total population can be marked (e.g., Macquarie Island, McMahon *et al.* 1999; and Pensinsula Valdés, Pistorius *et al.* 2004). Additionally, marking at Marion Island (this study) has extended longer than the maximum life span of this species (Hindell and Little 1988) and therefore, under two of the most fundamental closed population mark-recapture assumptions (no dispersal and no marker loss, Pollock 2000), all individuals in this study population should be marked. However, in long-term studies, these assumptions are generally not feasible (Pollock 2000) and more realistic (open) population models allow for additions or deletions representing immigration, emigration and marker loss, together with recruitment and mortality. The large number of untagged seals at Marion Island therefore requires scrutiny to assess the validity of some of these basic assumptions. Knowledge of the origin of the untagged population component is vital if their potential impact on population parameter estimation is to be gauged.

 Elephant seals are commonly marked by double-tagging in the hind flipper and tag-loss is an unavoidable component of long-term mark-resight programmes. Tag-loss rates have been estimated at Marion Island (Wilkinson and Bester 1997, Pistorius *et al.* 2000, Oosthuizen *et al.* 2010) and elsewhere (e.g., McMahon and White 2009) to adjust mark-resight survival estimates for the loss of marked individuals from the population (e.g., Pistorius *et al.* 1999, de Bruyn 2009). At Marion Island, tag-loss is low (lifetime cumulative inner interdigital tag-loss of 11.9 % for females and 18.4 % for males, Oosthuizen *et al.* 2010) and estimates do not predict the high numbers of untagged seals that are observed. A potential pitfall in these methods is the underestimation of tag-loss rates due to violations of the assumption that the loss rate of each tag on an individual seal is independent (see McMahon and White 2009) - a widespread limitation as permanent marking is often unattainable. Approximation of dispersal rates (immigration and emigration) have, in comparison, been neglected owing to the difficulty in quantifying these parameters (Nathan 2001) and because elephant seals have high site fidelity (usually return to their native island to haul out; Nicholls 1970, McMahon *et al.* 1999, Hofmeyr 2000). Yet, some degree of inter-island movement within the southern Indian Ocean is known to occur (Bester 1989, Guinet *et al.* 1992, see also Chapter 6). Both tag-loss and dispersal therefore add unmarked individuals to the Marion Island population, although they are predicted to add individuals to different sectors of the population (e.g., tag loss is expected to add unmarked individuals to adult age categories, while dispersal is predicted to add juvenile individuals to the population). The present study explores the origin of the untagged component of the population as expressed by tag-ratios.

Monthly fluctuations in tag-ratios followed the pattern predicted by differences in site fidelity between seal age classes and different haulout phases (Hofmeyr 2000). The highest tag-ratios were recorded for breeding females and lower tag-ratios were observed during the moult and especially the winter haulout. Elephant seals moult sequentially according to age and breeding experience (Hindell and Burton 1988, Kirkman *et al.* 2003) and tag-ratios reflected this sequential pattern of juveniles, adult females and adult males during the moult haulout (November - March). Tag-ratios increased in December from the principal juvenile moult phase in November and reached a peak during January (predominantly adult female moult haulout), before declining to the lowest levels (for the moult) during the adult male moult haulout (February to March). The increased presence of untagged seals during the juvenile moult corroborates findings of lower site fidelity in juvenile seals in comparison to adult females during the moult (Hofmeyr 2000) and previous observations of dispersing individuals

which mostly included juvenile seals hauling out on non-native islands during non-breeding haulouts (Bester 1989, van den Hoff 2000, Chapter 6). The low tag-ratio for moulting adult males is not unexpected as adult males repeatedly disperse to alternative non-breeding haulout sites during the moult. Some males from Heard and Macquarie islands moult at the Vestfold Hills and Windmill Islands in Antarctica for example (Burton 1985, Bester 1988, van den Hoff *et al.* 2003), whereas males breeding on Îles Kerguelen have moulted at Marion Island (see Chapter 6).

The lowest proportion of tagged seals (< 30%) occurs during the facultative autumn/winter or mid-year haulout (the purpose of which is still unclear) when juveniles are the principal age class ashore. Participation in the winter haulout differs by age and sex (except among under-yearlings, Kirkman *et al.* 2001, Field *et al.* 2005) and although not correlated to future survival, participation in the winter haulout may increase (or be associated with) higher site fidelity (Pistorius *et al.* 2002). Annually, more than 50% of surviving under-yearlings born at Marion Island and more than 60% of surviving yearlings (both sexes) haul out to winter at the natal site (Kirkman *et al.* 2001). Juvenile males aged two to four continue to haul out during winter in high proportions (Kirkman *et al.* 2001), but even so, untagged seals still outnumbered tagged seals three to one during this phase.

From 1997 to 2009, the number of untagged seals recorded at Marion Island increased relative to the number of tagged seals. If untagged seals at Marion Island are primarily migrants or immigrants, the decrease in tag-ratios may be associated with the stabilization and increase of elephant seal populations at Îles Kerguelen (since 1987) and Îles Crozet (since 1990, Guinet *et al.* 1999). Increasing source populations at Îles Kerguelen and Îles Crozet (assumed to incorporate improved survival rates) are hypothesised to result in greater emigration rates to Marion Island. However, these findings also fit with a change in the tagging protocol at Marion Island. Since 2000, elephant seal pups were marked by tagging in the upper, outer interdigital webbing of the hind flipper (to improve tag resighting), rather than the inner interdigital webbing of the hind flipper (1983 - 1999). The new tag site appears to have higher tag-loss rates (Oosthuizen *et al.* 2010) and will consequently result in more native untagged seals.

The greatest proportions of tagged seals hauled out on the northeastern coastline and on relatively isolated sites at Goodhope Bay (26), Kildalkey Bay (20) and Funk Bay (18, see

Figure 3.6 for locations). Spatial variation in tag-ratios was strongly coupled to the relative proportions of adult and juvenile seals that utilize the sites. Goodhope, Kildalkey and Funk bays are all major breeding sites on the southern coastline while the zone of high tag-ratios on the northeastern aspect include important breeding sites at Sealers' Beaches (62), King Penguin Bay (56) and Goney Beaches (53) amid numerous smaller breeding and non-breeding haulout sites. Generally, the presence of large numbers of breeding females will increase the tag-ratio for a specific site, biasing this analysis towards important breeding sites (Archway Bay (7) on the east coast, however, did not differ from the expected mean even though it is a major breeding site). We repeated the analyses using under-yearling and yearling haulouts only and obtained similar results. Beaches on the eastern and southern coast (including Funk and Kildalkey bays for under-yearling and yearlings only) had lower than expected tag-ratios; Goodhope Bay and beaches on the north-eastern aspect had higher than expected tag-ratios. Spatial differences are therefore likely to be influenced by numbers of female breeders (and consequently numbers of tagged pups added to the study population per annum per site), with variation in site specific fidelity (juveniles returning to the vicinity of their natal sites, Hofmeyr 2000) maintaining differences in numbers of tagged seals for all age classes on different sections of the coastline. Untagged seals thus appear to be distributed evenly amongst sites rather than occurring in greater numbers at large breeding sites (which would have a homogenising effect on tag-ratios between sites). Variation in this pattern may be caused by different physical characteristics (physiognomy) of different sites (Mulaudzi *et al.* 2008, Setsaas *et al.* 2008).

In summary, unmarked seals at Marion Island are most common (relative abundance) during the winter/mid-year haulout, followed by the moult and lastly the breeding season. The youngest age classes have the lowest proportion of tagged seals, and adult females the highest. These patterns suggest that the majority of unmarked seals are migrant seals, rather than seals native to Marion Island. Untagged seals haul out in greater numbers than tagged seals during non-breeding haulouts, perhaps indicating that these seals forage in the region of Marion Island (rather than near their native island) and haul out here during the winter (possibly to alleviate intra-specific competition [Field *et al.* 2005]) and to moult. Breeding dispersal of elephant seals between Marion Island and other islands is generally assumed to have negligible influence on population parameters (Pistorius *et al.* 1999, but see Bradshaw *et al.* 2002) or population trends (McMahon *et al.* 2009) even though the substantial positive consequence of immigration (as little as four breeding females per year) have been

demonstrated through population modeling (McMahon *et al*. 2005b). Some degree of inter-island movement does occur between Marion Island and neighbouring Prince Edward Island (Oosthuizen *et al.* 2009), Îles Crozet and distant Îles Kerguelen (Bester 1988, 1989, Guinet *et al*. 1992, Chapter 6), however, as a consequence of inadequate observer effort both spatially and temporally, movement-rates amongst these islands remain difficult to quantify. A proportion of the large number of migrant juvenile seals at Marion Island during non-breeding haulouts is expected to permanently immigrate to the breeding population (suggested by the proportion of untagged breeding females). The recent inflexion in population growth of elephant seals at Marion Island from stability to increase (McMahon *et al.* 2009) could perhaps be attributed to an increase in immigrant seals (from increasing populations at other islands) accompanied by improved survivorship of Marion Island seals (de Bruyn 2009). Spatially, untagged seals distribute evenly among haulout sites, while tag-ratios reflect high local site-fidelity of tagged seals.

The current analysis was facilitated by the long-term mark-resight programme at Marion Island (Bester 1988). Migrant seals appear to be abundant at the site, but as untagged migrant seals clearly do not form part of the marked population, their presence will not result in spurious survival rates estimated from the marked population. Population projections from mark-resight survival and fecundity rates may, however, not correlate to observed total population trends, as immigrant seals are an additional source of seals, including breeders (Bester 1989, de Bruyn 2009, Chapter 6). The mark-resight schedule at Marion Island should continue to include all beaches where elephant seals haul out as concentrating effort on subsections of the coastline, for whatever reason, would clearly be less productive (this study).

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