



Frontispiece. A 23-year old branded elephant seal, seen nursing a pup at Macquarie Island in 1985. Photograph courtesy of Mark Hindell

*“Our object in studying Nature is to be faithful to our experience of her.
We do not want to recreate Nature in our own image, and as far as possible
we wish to eliminate errors of observation or construction which are due to
us as observers”*

Jan Christian Smuts (Holism and Evolution, 1926)

A DEMOGRAPHIC COMPARISON OF TWO
ELEPHANT SEAL POPULATIONS

by

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Submitted in partial fulfilment of the requirements for
the degree of

PhD (Zoology)

in the

Faculty of Natural and Agricultural Sciences

University of Pretoria

September, 2002.

Declaration

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief, no material previously published or written by another person except where due acknowledgement is made in the text of the thesis.

Clive McMahon

Dedication

To my parents; Frank and Ina and in memory of my grandparents; Carl and Sophie and Frank and Rina

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ABSTRACT

The demography of two elephant seal populations was examined and compared. This was done to investigate the reasons for the observed decreases in populations at Marion and Macquarie islands.

While a well-established demographic programme had been in place at Marion Island since the 1980's (see Pistorius *et al.* (1999a) for a review) one had to be established at Macquarie Island. A long-term demographic programme was initiated at Macquarie Island in 1993 and hot brands were used to mark seals. Hot-iron branding was a rapid and reliable method of permanently identifying elephant seals that did not prejudice survival and did not appear to cause undue stress (in the short-term). Neither branding nor handling showed any long-term effects as measured by survival after one year.

From the inter-island comparison of survivorship, age at first breeding and wean mass I concluded that the observed decreases in elephant seal numbers between the 1950s and 1990s in the Pacific and Indian Ocean sectors were driven by resource limitation in the Southern Ocean. A conglomerate of factors including local predation by killer whales and intra-specific resource competition was postulated as a cause for the inter-island (regional) differences in population trends. Presently it appears that *per capita* more resources are available to the Marion Island population than are available to the Macquarie Island population.

The vital rates that had the greatest impact (elasticity) on fitness (population growth) for all populations i.e. Marion Island, Macquarie Island and South Georgia, were, in order of importance: (1) juvenile survival, (2) adult survival, (3) adult fecundity and (4) juvenile fecundity. At Marion Island juvenile and adult survival contributed equally to the fitness of the population while at Macquarie Island and at South Georgia Island juvenile survival was more important than adult survival in determining population fitness.

The global population of elephant seals in 2001 was estimated at approximately 738 772 which represents an increase of 11% from the last world estimate (664 000).

It seems clear from the evidence presented and reviewed here that the present changes in seal populations, unlike the period of direct exploitation in the 19th and 20th centuries, are neither a consequence of direct human interactions nor present-day commercial activities.

While the significance of inter-specific competition between elephant seals and other Antarctic predators remain largely unknown or quantified, it would seem prudent that these relationships be studied. This is because resource competitors (toothed whales) have been increasing in number since the cessation of commercial whaling.

Even though elephant seals are considered the most studied of all pinnipeds (Ling & Bryden, 1992) much remains to be learnt. Foremost are to gain a clear understanding of the *in situ* diet of elephant seals and to assess the role pathogens play in the regulation of seal populations. In addition to these studies it is also important that the current long-term monitoring programmes at Marion and Macquarie islands continue, as they provide valuable base line information on the fate of elephant seal populations.

ACKNOWLEDGEMENTS

I would like to thank my supervisor Prof. Marthán Bester and co-supervisor Mr. Harry Burton, for their advice and encouragement during the course of this study. Their kindness, friendship and professional help have been invaluable. In addition to my supervisors I would like to thank Dr. Mark Hindell for his enthusiastic support of the project, his insightful discussions and his friendship.

The data presented here were collected over many years and by many people at Marion Island and at Macquarie Island, and for this support from my colleagues and friends I am eternally grateful. I am indebted to my colleagues of all the Australian National Antarctic Research Expeditions (ANARE) to Macquarie Island and all the South African National Antarctic Program (SANAP) expeditions from 1993-2001 to Marion Island that so ably assisted me in the field by marking seals and collecting resights in often miserable conditions. Your professionalism and friendship in the field, and later in the laboratory were truly encouraging, and may the insights presented here always stand as a testament to your help.

To my friends in Hobart; Jack, Barbara, Maddy and Jonathan, Rags, Suzi, Josh, and Harry, Smudge, Fabio, Malcolm, Donald, and Cecelia my sincere thanks to you all for your friendship and the many inspirational discussions. I would especially like to thank John (a.k.a. Snake) for his unfailing sense of humour and friendship.

Finally I wish to thank Louise for her encouragement and support throughout this project. I am indebted to her for enduring the many months of separation during the time I was on Macquarie Island.

This study was supported logistically by the Australian Antarctic Division, and financially by the University of Pretoria through a PhD scholarship. The Australian Antarctic Animal Ethics Committee (AAS 2265) and the Tasmanian Parks and Wildlife Service approved and permitted all aspects of this research at Macquarie Island. The Ethics Committee of the Faculty of Natural and Agricultural Sciences (etiek@scientia.up.ac.za) of the University of Pretoria endorsed the research at Marion Island (Reference number EC 990112-002) under permit from the Director-General: South African Department of Environmental Affairs and Tourism.

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Chapter 1 - Introduction

General Introduction

The southern elephant seal (*Mirounga leonina* Linn.) is one of the more numerous pinniped species in the world and much research and scientific interest has been focussed on this animal. This has been due largely to the accessibility of the seals to researchers and the predictability of the haulout and breeding behaviours of the seals, which are the same reasons that have made the seals attractive to earlier harvesting by sealers. Initially the contact between humans and seals was a one of economic exploitation by man (Busch 1985). Elephant seals were seen as an exploitable resource, for high quality oil derived from their blubber deposits, at all their major breeding grounds (Bonner 1989). This hunting greatly reduced many populations (Laws 1994). However, a decline in the world market of seal oil and the reduction in the trade in fur seal skins resulted in the abandonment of much of the elephant seal hunt, which allowed most populations to recover, like at Macquarie Island (Hindell & Burton 1987).

The annual cycle of the southern elephant seal involves two periods at sea that are punctuated by two periods ashore, one for activities associated with reproduction, and the other for the moult. This behaviour has resulted in some aspects of the terrestrial phase of their life cycle having been studied in detail investigating their ecology (Bester & Wilkinson 1994; Carrick 1964; Carrick & Ingham 1960; Hindell 1991; Laws 1956a; McMahon *et al.* 2000; Pistorius *et al.* 1999a), behaviour (McCann 1981; McCann 1982; McCann & Rothery 1988), development, (Bryden 1968a; Bryden 1968b; Bryden 1968c; Guinet 1991; Hindell *et al.* 2000; Irvine *et al.* 2000) and energetics (Boyd *et al.* 1993; Carlini *et al.* 1999; Carlini *et al.* 2001; Fedak *et al.* 1994; Hindell & Slip 1997; Hindell *et al.* 1994a). Since 1987, the availability of archival and satellite linked recording devices has increased the number of studies concerned with the marine phase of the annual cycle of the elephant seal. These studies have provided information on the dive behaviour, and the movement patterns of elephant seals from Macquarie Island (Field *et al.* 2001; Hindell *et al.* 1991a; Hindell *et al.* 1991b; Hindell *et al.* 1999; McConnell *et al.* 2002; Slip *et al.* 1994), Marion Island (Bester 1989; Jonker & Bester 1994; Jonker & Bester 1998), South Georgia (Boyd & Arnborn 1991; McConnell *et al.* 1992; McConnell & Fedak 1996) and Patagonia (Campagna *et al.* 1995; Campagna *et al.* 1998). More recently with the development of advanced demographic tools such as the mark-recapture program MARK (White & Burnham 1999), and the realization that elephant seal populations at many breeding locations were decreasing or of unknown status, studies have concentrated on describing the status of individual populations and on determining the key life-history parameters driving population change (Boyd *et al.* 1996;

Guinet *et al.* 1999; McMahon *et al.* 1999; Pistorius *et al.* 1999a; Pistorius *et al.* 1999b; Pistorius *et al.* 2001).

Biology of the Southern Elephant Seal

The southern elephant seal, *M. leonina*, is the largest species of the world's 34 extant species of pinnipeds (King 1983) and is sexually dimorphic. Reproductive adult males can be over 5 metres in length and weigh between 1,500 and 3,000 kg, with maximum mass reaching 3700 kg (Ling & Bryden 1992), while adult females range widely in mass from 350 to 800 kg (soon after giving birth); but most weigh between 400 and 600 kg (Fedak *et al.* 1994). Southern elephant seals give birth and breed in September-November, the larger males arriving a month before the females and other males in order to fight for dominance and the right to a harem of females (Ling & Bryden 1992). Only the largest 2-3% of males each year gain this right and successful males may have access to more than 100 females (McCann 1981). The female usually gives birth between 0-10 days after coming ashore (Carrick *et al.* 1962a; Laws 1956a). Mothers typically give birth to a single pup (Laws 1953; Spotte 1982), but twinning, although rare, has been reported (Arnbom *et al.* 1997; Bryden 1966; McMahon & Hindell 2002). Mean pup mass at birth ranges between 34 kg and 49 kg, and mean pup mass at weaning varies between 98 kg and 171 kg depending on sex and location (Burton *et al.* 1997). The lactation period also apparently varies among populations ranging from about 21 to 24 days (SCAR 1991). The mass of pups at weaning depends largely on the mass of the mother at the start of the breeding season (Arnbom *et al.* 1994; Arnbom *et al.* 1997; Fedak *et al.* 1996). Once pups are weaned they stay on shore fasting for about 9 weeks, leaving their natal islands when their mass reaches about 70% of their weaned mass (Arnbom *et al.* 1993; Wilkinson & Bester 1990).

Distribution of Southern Elephant Seal Populations

The southern elephant seal has a circumpolar distribution and breeds on sub-Antarctic islands that are close to the Antarctic Polar Front (Laws 1994; Ling & Bryden 1992). Initially three main southern elephant seal stocks were recognized: the South Georgia stock, the Macquarie Island stock, and the Kerguelen stock (Laws 1960). But, through the advent of molecular techniques it is now acknowledged that there are four genetically distinct stocks: the Peninsula Valdés stock in Argentina, the South Georgia stock in the South Atlantic Ocean, the Kerguelen stock in the south Indian Ocean and the Macquarie stock in the South Pacific Ocean (Hoelzel *et al.* 2001; Slade *et al.* 1998). The principal breeding colonies for these stocks are located on: Peninsula Valdés, South Georgia Island, Heard Island and Îles Kerguelen, and Macquarie Island respectively (Fig.1.1).

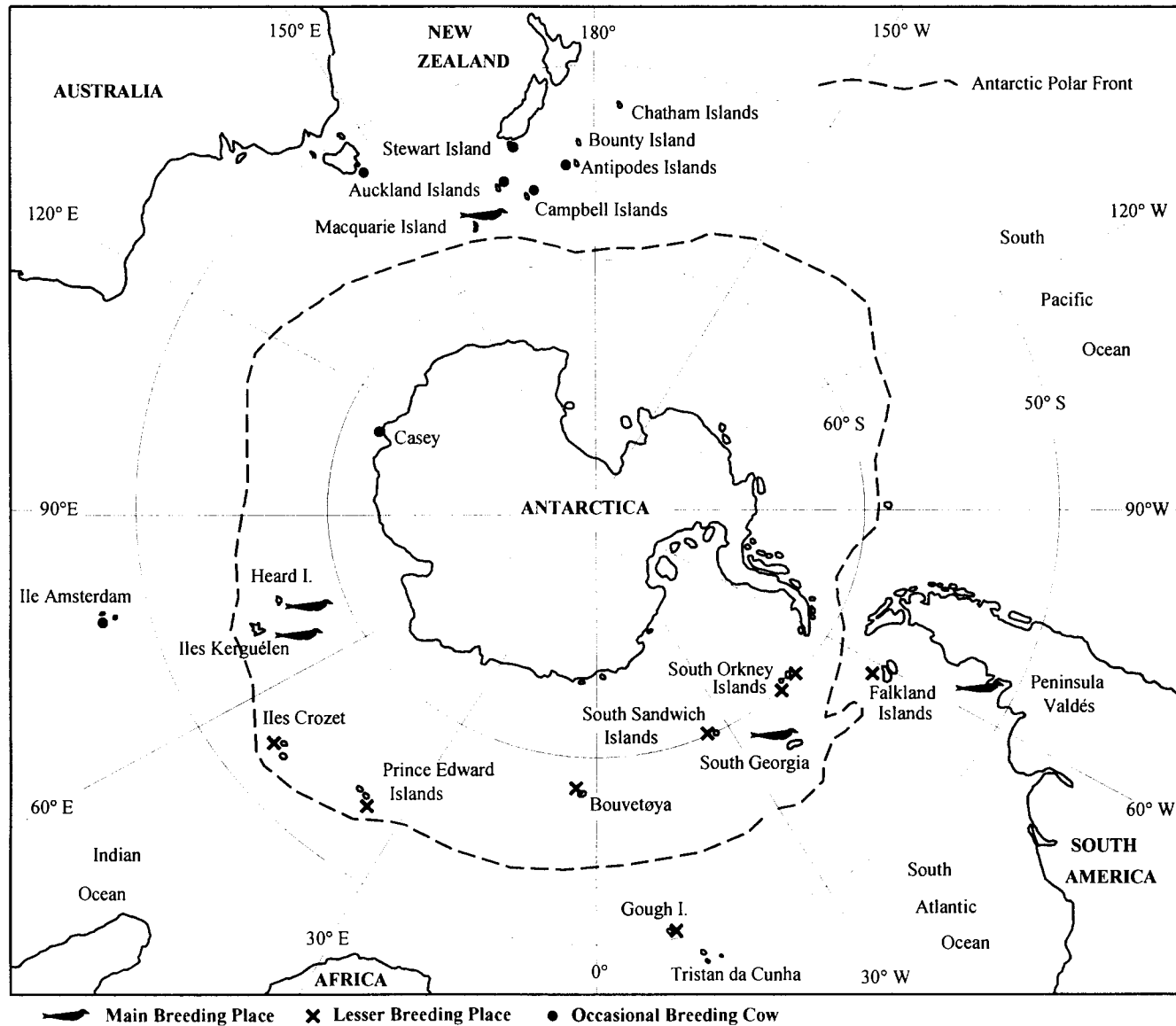


Figure 1.1. The circumpolar breeding distribution of the southern elephant seal.

The South Georgia stock is the largest numerically, accounting for over half of the world population, and includes breeding colonies in the Scotia arc (South Georgia, South Orkney Islands, South Shetland Islands, South Sandwich Islands), together with Gough Island and Bouvetøya (Laws 1994). While there is little overlap between these stocks on land at breeding colonies and hence little exchange of genetic material there are some indications of overlap at moulting locations (e.g. Bester 1988; Guinet *et al.* 1992a; Hindell & McMahon 2000; Laws 1994). The degree of overlap and distribution of populations at sea remain unknown.

Distribution at Sea

Southern elephant seals dive almost continuously while at sea, diving deeply, and travelling long distances away from their breeding islands (Bester & Pansegrouw 1992; Boyd & Arnbom 1991; Campagna *et al.* 1998; Hindell *et al.* 1991a; Hindell *et al.* 1991b; Hindell & McMahon 2000; Jonker & Bester 1998; McConnell & Fedak 1996; McConnell *et al.* 2002). Adult and juvenile seals travel long distances for prolonged periods at “straight line” speeds of around 70 - 80 km/day, interrupted by periods where they are relatively stationary (Campagna *et al.* 1998; Hindell *et al.* 2000; Hindell & McMahon 2000; Jonker & Bester 1998; McConnell & Fedak 1996; McConnell *et al.* 2002). Because of their ability to travel large distances, vast areas of the Southern Ocean are available to elephant seals. Seals may use static physical features that are associated with high densities of prey, such as the continental shelf break, in order to locate prey (McConnell *et al.* 1992; McConnell & Fedak 1996; McConnell *et al.* 2002). The oceanographic features around the main elephant seal breeding islands are also different. For example, Macquarie Island and Marion Island are on mid-ocean ridges with very little surrounding shelf area, South Georgia has more shelf area and is relatively close to the Antarctic Peninsula, and Heard Island is on the Kerguelen Plateau (Gordon & Molinelli 1982). These differences suggest that elephant seals from each island may have differences in their diving behaviour and movement patterns.

Past and Present Status of Elephant Seal Populations

Most southern elephant seal populations were harvested for their oil at some time in the eighteenth, nineteenth and early twentieth centuries (Busch 1985; Hindell & Burton 1987). The extent and timing of sealing differed among populations. Many examples exist but the point is best illustrated by: the complete elimination of elephant seals from the Bass Strait islands of southern Australia in the 1800's (Bryden *et al.* 1999; Ling 1999), the prolonged exploitation of

the Macquarie Island population from 1810 until 1919 (Cumpston 1968), and the brief exploitation at Heard Island from 1855 to 1881 (Downes 1996). South Georgia was visited by sealers before 1800, and sealing occurred there in the nineteenth century (Busch 1985), then in the twentieth century sealing occurred there under license from 1910 to 1964 (Laws 1994). The extent and the impact of the unregulated sealing is unknown but was estimated from shipping logs to have been severe, with the population at Macquarie Island reduced by about 70% (Hindell & Burton 1988a).

Overall, the southern Pacific and southern Indian Ocean southern elephant seal populations have decreased (Barrat & Mougín 1978; Burton 1986; Condy 1978; Guinet *et al.* 1992; Hindell 1991; Hindell & Burton 1987; Pistorius *et al.* 1999b). While the decline at Îles Kerguelen has reversed, (Guinet *et al.* 1999) it has apparently stabilized at Heard Island (Slip & Burton 1999) and possibly at Marion Island (Bradshaw *et al.* 2002; Pistorius & Bester 2002a; Pistorius *et al.* 2001). However, the population continues to decline at Macquarie Island (Hindell *et al.* 1994b). In contrast to the southern Indian and Pacific Ocean populations, the southern Atlantic Ocean populations at South Georgia, the Falkland Islands and Peninsula Valdés have remained stable or increased (Boyd *et al.* 1996; Campagna *et al.* 1993; Galimberti & Boitani 1999; Lewis *et al.* 1998), with only the very small population at Gough Island showing a long-term decline (Bester *et al.* 2001). The cause(s) for the decrease in the southern Pacific Ocean population remain(s) unknown, although it may potentially be similar to that at Marion Island where food limitation has been implicated (Pistorius *et al.* 1999b).

Thesis Structure and Aims

This study investigates the demographic structure of two decreasing populations of southern elephant seals at Macquarie Island and Marion Island. In order to study the life history of living organisms (seals in this instance) individual seals need to be marked either at birth or shortly thereafter and followed throughout their lives, so that individual capture-mark-recapture histories can be constructed. These capture-mark-recapture histories then provide the basis for the study of age-specific survival for individual seals. There are many ways to mark seals, each with a set of advantages and a set of limitations. Chapter 2 – branding- describes and assesses the marking techniques used in the present study. Because research activities can be seen as invasive and/or disruptive and because researchers aim to have minimal impact on research subjects, Chapter 3 reviews the consequences of handling seals to mark them and subsequently recapture (here recapture is used to mean resight) them. The generality of the methods and data presented in the

proceeding three chapters offer insights that are applicable to the study of other seal taxa and also other mammal taxa. Having established the appropriate marking methods and the impact of these methods on seal survival, Chapter 4 compares the survival of five concurrent cohorts of seals to age seven at Marion Island and at Macquarie Island. By studying two declining populations I aimed to identify characteristics common to both populations as a means of elucidating the causal parameters that may be driving/ have driven the population declines. To achieve this I:

- 1) Assessed the concurrent age-, sex- and cohort-specific survival of the two populations.
- 2) Determined the rates of juvenile and adult survival and compared the survival rates at Macquarie and Marion islands.
- 3) Calculated the age at first breeding for each site and compared the results.
- 4) Proposed a hypothesis that describes the causal factors driving elephant seal declines.

How these survival rates and fecundities affect and/or drive population change has been contentious and two principal schools of thought exist: (1) that adult (particularly female) survival is important (Galimberti & Boitani 2001; Pistorius & Bester 2002a; Pistorius *et al.* 1999a; Pistorius *et al.* 1999b) and (2) that survival of juvenile seals and their recruitment into the breeding population are the principal driving forces (Hindell 1991; McMahan *et al.* 2003). Such contentions about causes of population changes are not uncommon. However, mathematical population models provide a means to test the relative contribution that each hypothesis makes at the population level. Thus to assess the validity of each hypothesis Chapter 5 had two primary aims: (1) to simulate/project the population growth rates for three southern elephant seal populations using life table information and (2) to discover and describe the critical components in determining fitness (population growth rate) for each population. To achieve these goals I formulated a stochastic population matrix model, using matrix algebra, based on a Leslie population matrix. The final chapter, Chapter 6 is a synopsis of what is currently known about southern elephant seals and also provides an overview of prospective future research. Because of the vast body of work that has followed since the previous overviews (Hindell *et al.* 1994b; Laws 1994), Chapter 6 is an update that incorporates findings and hypotheses from recently published work.

The chapters of this thesis were prepared as separate papers, and this has led to a certain amount of repetition in the introduction and methods sections of some of the chapters. However, with

regard to the preparation of the papers and subsequent chapters of the thesis I was always the senior author and took responsibility for data collection (directly or under my direct supervision), analysis, and presentation. The fieldwork was conducted concurrently at Marion Island and Macquarie Island from 1993-2001.

Chapter 2 - Hot-iron branding as a reliable means of permanently marking seals and it's effect on southern elephant seal heart-rate

Introduction

The process of marking otherwise indistinguishable seals as individuals (and following them through subsequent phases of their lives) has been central to numerous advances in seal ecology. These include calculating growth rates (Bell *et al.* 1997a; Carrick *et al.* 1962a; Kovacs & Lavigne 1986; Pomeroy *et al.* 1999), recording breeding success (LeBoeuf 1972; Lenarz & Shaw 1997; Reiter *et al.* 1981; Testa 1987), identifying migratory and dispersion patterns (Bester 1988; Harwood *et al.* 1976; Hindell & McMahon 2000; Ingham 1960; McMahon *et al.* 1999; van den Hoff 2001), calculating senescence (Pistorius & Bester 2002b), longevity (Hindell & Little 1988) and survival (Aurioles & Sinsel 1988; Caughley 1977; Hindell 1991; McMahon *et al.* 2000; Pistorius *et al.* 1999a; Schreer *et al.* 1996; Seber 1973; Seber 1986; Testa & Rothery 1992b; Wilkinson & Bester 1997).

Accurate survival estimates are essential for assessing the conservation status of animal populations (Lebreton *et al.* 1992). Survival may be under-estimated if individual identifying marks are lost and surviving animals are consequently not recognised (Eberhardt *et al.* 1979; Frazer 1983; Lebreton *et al.* 1992; Seber & Felton 1981). Therefore permanent and legible marks on animals are of paramount importance. A number of pinniped studies have used flipper tags for identification but few have described their effectiveness (e. g. Bradshaw *et al.* 2000; Pistorius *et al.* 2000; Testa & Rothery 1992b; Wilkinson & Bester 1997). There are several other methods of marking seals (Erickson *et al.* 1993), but like tagging, these methods are temporary or the identifiers are difficult to read. Current PIT (passive integrating transponders) tags, for example, require that the tag-reading head of the probe be placed very close (usually within ~ 20cm of the animal's body) for the signal from the tag to have a good chance of being received (Clarke & Kerry 1998). In one study of southern elephant seals, PIT tags had a ~2.2% failure rate but are considered an effective back up to other marking methods (Galimberti *et al.* 2000b). However, because seal harems are large, dense congregations of seals it seems likely that searching for marked seals marked by PIT tags would be highly disruptive in nature. Without an external marking, each seal must be checked for it's internal tag on each assessment occasion where the marked individuals may be 20 metres inside the harem perimeter and thus essentially unidentifiable on that date. If there is an external marking then presumably the internal tag is not necessary. Problems such as those outlined above are largely overcome by branding (Carrick &

Ingham 1962b; Erickson *et al.* 1993; Harwood *et al.* 1976; Merrick *et al.* 1996; Pomeroy *et al.* 1999).

Southern elephant seals were first hot-iron branded at South Georgia in the 1920s when 2000 seals were marked (Matthews 1929). Grey seals (*Halichoerus grypus*) were branded in Wales in 1946 and individuals were resighted more than a decade later (Lockley 1966). The Australian National Antarctic Research Expeditions (ANARE) then used this technique to mark southern elephant seals at Heard and Macquarie islands in the 1950s and 1960s for demographic studies (Carrick & Ingham 1962b; Chittleborough & Ealey 1951; Csordas 1964; Ingham 1960; Ingham 1967). These papers were the first to identify individual southern elephant seals and their cohorts and age-groups from the Southern Ocean without the necessity of killing to age them from their teeth, e.g., as was done at South Georgia (Laws 1956b). However, these studies from Macquarie and Heard islands did not comment on the results that branding had on seal survival or on the extent of “brand loss”.

Here I describe the hot-iron branding technique and equipment used to permanently mark a proportion of the southern elephant seal population at Macquarie Island. I assess the efficacy of hot-iron branding for long-term demographic studies and determine the impact branding had on survival by calculating the survival for branded and unbranded (but tagged) seals. I also calculate first-year survival for seals with healed brand-marks and those with unhealed brand-marks. The heart rates of five pups were measured prior to branding, during restraint, during branding, and on two occasions after branding and released to determine the specific reaction of seals to branding. As an alternative to hot-iron branding, cryo-branding was tested.

Methods

Approximately 19 000 elephant seal pups are born each year on the beaches at Macquarie Island (54° 30' S 158° 50' E) between September and November (ANARE unpublished data). Of these, approximately 10% (2 000) were hot-iron branded annually, after weaning in November, over a seven-year period (1993-1999). Pups wean after approximately three weeks (24.52 days \pm 2.7) (McMahon *et al.* 1997). One thousand of the seals branded each year were tagged within 24 hours of birth in their hind flippers with two uniquely numbered plastic tags (McMahon *et al.* 1999; McMahon *et al.* 1997). Tags were inserted into the inter-digital webbing between the first and second digits of both rear flippers. The tags were placed approximately 25 mm from the trailing edge of the flipper. Therefore a total of ~7 000 pups had double markings (branded and tagged)

after weaning. Thus brand resights could be verified from the flipper tags if they were present. Near daily surveys of the isthmus (site where seals were born and subsequently marked) and monthly surveys of the entire island were made to record the presence of branded seals (McMahon *et al.* 1999).

Branding Technique

Weaned pups that had completely moulted their black pup fur to the adult, grey hair were selected for branding. This had occurred by three weeks after weaning. Each seal was branded with a three-digit number and a letter prefix on each side of their caudo-dorsal flanks (Fig. 2.1). Particularly small weanlings (<60 kg at weaning) were given only one brand, on the dorsal midline. The letter prefix denoted membership of a particular cohort, while the number uniquely identified the seal. This meant that four individual brand symbols were applied to each flank. Fifty millimetre cast-iron cattle brands were used (Fig 2.2). These were essentially identical to those used in previous studies at Macquarie and Heard islands (Carrick & Ingham 1962b; Chittleborough & Ealey 1951; Csordas 1964; Ingham 1960; Ingham 1967). All the sharp ends and corners on the cast brands were ground down to curved profiles. The brands (Fig 2.3) were mounted in two carriers (Fig 2.4) attached to a 780 mm-long mild-steel rod handle and heated over a gas (Liquid Petroleum Gas [LPG]) brazier protected by a metal housing that was mounted on the back of a tractor. The tractor was positioned as close to the seals as possible, to reduce heat loss from the brands as they were carried from the brazier. A team of four people restrained and branded the seals. Two people restrained the seal, one straddling the head and restraining the fore flippers and the other restraining the hindquarters. The third person heated, changed brands and branded, whilst the fourth person acted as a relief brander, kept the book records, and applied pressure to the flank opposite to that being branded. Brands were heated until they glowed cherry-red, approximately 700°C (Böhler Bros. annealing colour chart, Austria). All temperature changes were monitored by the change in colour of the cast iron as given in the annealing colour chart. Each seal's skin was brushed prior to branding to remove dirt and sand; and, in placing the brands on the flanks, wounds from the bites of harem females were avoided. The brands on 12 000 seals were held on the skin for three seconds for the first brand-mark and four seconds for the second brand-mark to compensate for a ~50-100°C reduction in iron temperature as the branding irons were moved to the opposite side (see results). However, in 1994 only, 2 000 seals were marked with cherry-red brands for two seconds on both flanks. In most years, brands were applied to the left flank first and, if not, then the side priority was noted. The brands were held on the skin for three or four seconds (as described above) with even pressure, irrespective of whether

the seals were wet or dry. After branding, the seals were released and the burns left to heal naturally.



Figure 2.1. A branded elephant seal (B718) at Macquarie Island showing the four character caudo-dorsal flank brand that individually identifies each seal. The letter prefix denotes membership to a specific cohort, while the numerals uniquely identify the seal. Note the size of the brand characters on this 5-year-old male.

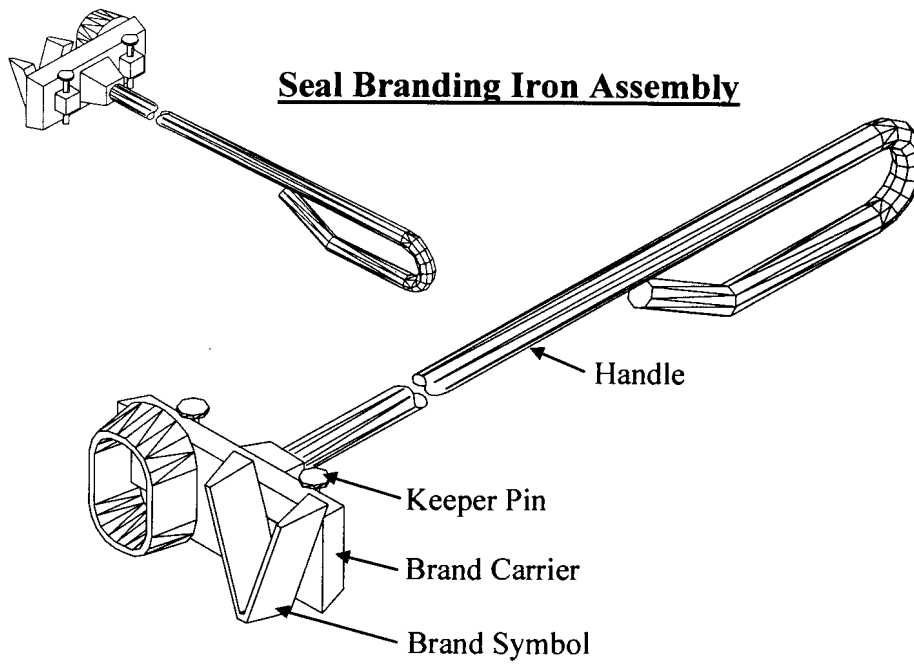


Figure 2.2. The branding irons used on southern elephant seals at Macquarie Island, showing the assembled brands, brand carrier and brand handle.

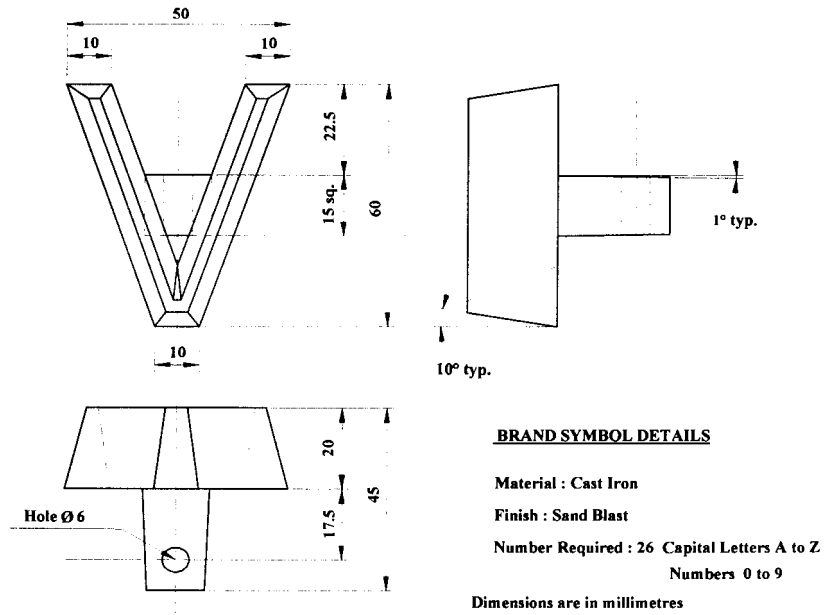


Figure 2.3. Dimensions and technical description of the cast iron cattle brands used on southern elephant seals at Macquarie Island.

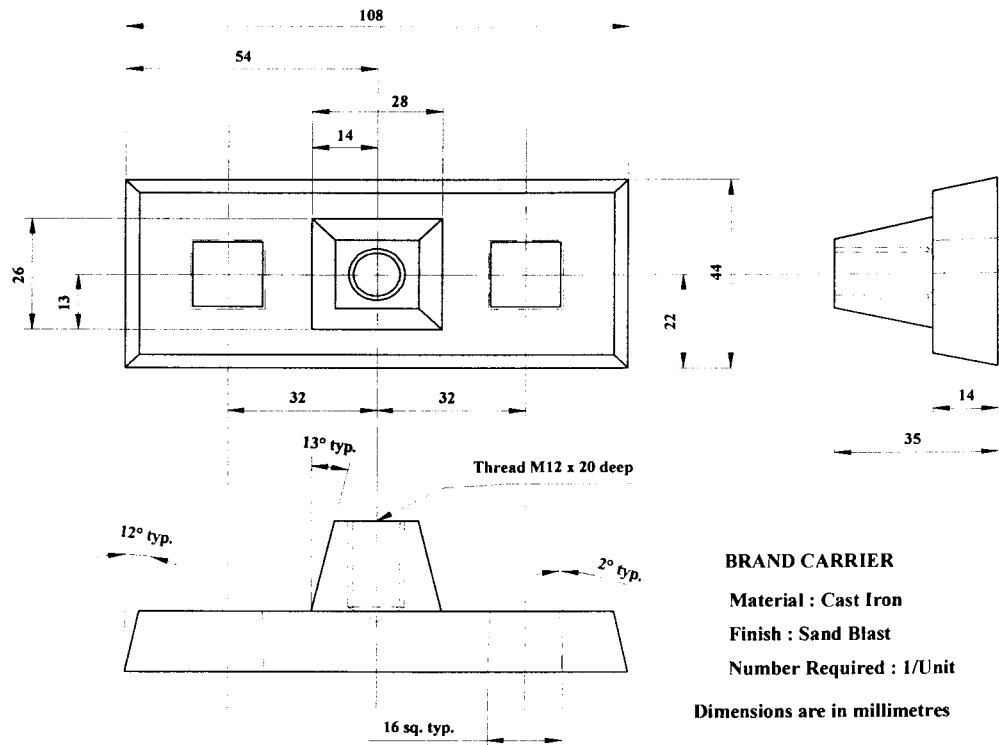


Figure 2.4. Dimensions and technical description of the cast iron cattle brand carriers used on southern elephant seals at Macquarie Island.

Brand-mark loss

Brand-mark legibility was assessed at the time of branding in 1998 and 1999. “Brand loss” was calculated by determining the number of branded seals with tags that could only be identified by their tag numbers at their first sighting. Brand loss (BL) was thus expressed as:

$$BL = \frac{I_s}{T_{bt}} \quad \text{Equation 1}$$

Where: BL = brand loss

I_s = number of tagged and branded seals that could not be identified by either brand.

T_{bt} = the total number of tagged and branded seals that were observed.

Survival estimates

First-year survival estimates for marked cohorts were calculated using the mark-recapture program MARK (White & Burnham 1999). The estimates of 1 000 tagged and branded seals was compared with the concurrently “tagged only” seals ($n = 172$). Furthermore the survival estimates for 7 000 branded seals (i.e. all tagged and branded seals from the 1993 – 1999 cohorts) was compared with 2 000 seals tagged only in the year 2000. The “tagged only” seal survivorship estimates were adjusted upwards by 2% to allow for the loss of both tags from some animals (AAD data). It was assumed that tagging had no effect on first-year survival as was the case for weaned Monk seal pups (Baker & Johanas 2002).

Starting from a general model which fits the data, the Akaike information criteria scores (AIC) and Δ AIC scores were used to select the most parsimonious model(s) (Burnham & Anderson 2001) and likelihood ratio tests within MARK were used to test specific hypotheses (Lebreton *et al.* 1992). As a rough guide Burnham & Anderson (2001) suggest that models with Δ AICs ≤ 2 have substantial support, those with Δ AICs of 4-7 have some support while those models with Δ AICs > 10 have no support.

Small wounds may result from branding (Chittleborough & Ealey 1951; Csordas 1964) and 1 513 seals from the 1998 cohort were classified as wounded or not-wounded at the time the seals were

branded. For the purposes of this study wounds in the brand area are defined as areas where the skin has been broken by the brand and some blubber is visible. A comparison between the estimated survival of seals with wounds ($n = 88$) with the estimated survival of seals without wounds ($n = 1\ 425$) was then made using MARK.

Comparisons of survival estimates can be compromised by resight effort (Caughley 1977) and it is likely that the estimates for tagged only seals (2 000) and the branded seal cohorts (1993-1999) may be subject to this bias. Therefore the resight effort between the two groups was standardised by using only the first 18 months of recaptures of each cohort.

Heart rates during branding

The heart rates of five seals were measured during hot-iron branding in 1999 using heart-rate data loggers (Sea Mammal Research Unit, St Andrews, Scotland) that had been attached with glue (Fedak *et al.* 1983; Hindell *et al.* 1991a; van den Hoff *et al.* 2002) to weaned pups several days prior to branding. The heart rate was displayed in an external window on the heart-rate logger. Heart rate was recorded at five stages of the branding process: 1) immediately prior to restraining the seal (resting heart rate), 2) during restraint, 3) on application of the brands, 4) two minutes following restraint, and 5) 10 minutes following restraint. The data were compared using ANOVA to detect general trends and a *post-hoc* Tukeys HSD test was used to determine specific differences.

Cryo-branding

In 1991, fifty weaned pups were cryo-branded in a pilot study to assess this technique to permanently mark southern elephant seals for long-term studies. Cast brass brands, 55 mm wide and 65 mm high were cooled in either dry ice or liquid nitrogen and applied to an area of skin that had been shaved of hair. Twenty seals were individually branded with two numerals cooled in dry ice and twenty were individually branded with two numerals cooled in liquid nitrogen. These forty seals were branded for 10 seconds. Another 10 seals were individually branded for 30 seconds. Five of these seals' brands were chilled with dry ice and the other five in liquid nitrogen. All 50 seals were double tagged with two uniquely numbered flipper tags in the inter-digital webbing of the hind flippers as described above.

Results

Branding Technique

Clear and legible brand marks resulted from branding weaned elephant seal pups using the techniques described here. As the seals grew, so too did the brand itself. At five years of age the 50 mm brand had reached a height of ~100 mm (Fig. 2.1) which made the seals more easily identifiable from greater distances.

Applying the brands for two seconds produced a clear brand at the time of branding; however, after the first moult, the result was often a faint and indiscernible brand which was difficult to read at any distance. This resulted in reduced recognition of the cohort branded in 1994. There was double the proportion (0.08) of unreadable brand marks from the 1994 cohort (when only two second brand times were used) compared to the proportion (0.04) from other cohorts.

Brand loss

From the resight records of observations of individual tags and brands on 4 862 branded and tagged seals, resighted between 1993 and 1999, 103 seals could only be identified from their tags and not from either of their brands. Indeed, this is a conservative approach because if either brand is illegible brand loss has occurred but the animal is not necessarily unidentifiable. Using Equation 1, I estimated overall brand loss to be 2.1%. This was a conservative estimate because This value is drawn from observations of animals with ages between two and seven years. Of the unreadable brands observed, 83% were too faint to read, and most of these faint brand-marks (78%) were the result of the two second brand application time trialled in 1994.

Survival estimates

Wounds that occurred at the time of branding did not affect seal survival ($\chi^2_3 = 0.006$, $p = 0.9$); and survival estimates for the wounded and unwounded groups were virtually identical ($67.34\% \pm 0.017$ and $67.43\% \pm 0.013$ respectively). No differences were detectable ($\chi^2_2 = 0.004$, $p = 0.99$) between the recapture probabilities of the two groups of seals. Neither the survival nor the recapture model that included group effects, i.e. splitting the wounded and unwounded seals, could be justified (Delta (Δ) Akaike's Information Criterion (AIC) = 6.01 and 7.95) (Burnham & Anderson 2001). The most parsimonious model was the one which did not distinguish between the survival and recapture rates of either group (Δ AIC = 0.0).

First year survival estimates for the 1996 and 1998 branded cohorts were similar (Table 2.1). First year survival for tagged only seals was less (62.1 and 60.3 % for 1996 and 1998 respectively) than that for the concurrently branded seals in 1996 (69.9 %) ($Z = 9.88$, $p < 0.001$) and 1998 (67.4 %) ($Z = 34.10$, $p < 0.001$) (Table 2.1). After standardising the recapture time between the recently tagged only seals (2000) with a short encounter history (18 months) and giving the 7 000 branded (1993 – 1999) seals an encounter history of the same length (18 months), the survival estimates were similar (Table 2.1). However, rather than differences between groups, i.e. tagged and branded seals ($\chi^2_1 = 0.789$, $p = 0.37$) differences in time, i.e. effort, were a more ($\chi^2_1 = 477.4$, $p = 0.0001$) appropriate way of quantifying search effort and describing survival. The model that best described recapture probabilities included both differences in mark type (i.e. branded vs. tagged) and search effort (AIC-weight 0.9 (group and time), 0.0 (time only) and 0.0 (group only)). Furthermore, a combined time and group model had a delta AIC (Δ AIC) of 0.0. The Δ AICs for the model containing only time effects was 36.2 and for the model with only group effects Δ AIC was 513. Thus the best model describing the differences in capture probability was the combined one.

Table 2.1. First year survival estimates (\pm SE) for branded seals and for tagged only seals at Macquarie Island. Estimates are corrected for brand and tag loss and for pre-weaning mortality.

Cohorts	1996	1998	2000
Survival estimates for branded seals	69.9%	67.4%	
	± 0.02	± 0.01	
Recapture rates for branded seals	54.7%	63.6%	
	± 0.01	± 0.01	
Survival estimates for tagged seals	62.1%	60.3%	67.8%
	± 0.09	± 0.12	± 0.005
Recapture rates for tagged seals	53.2%	57.7%	70.72%
	± 0.1	± 0.1	± 0.02
Survival estimates for wounded seals	N/A	67.34%	N/A
		0.02	
Survival estimates for unwounded seals	N/A	67.43%	N/A
		± 0.01	

Heart rates during branding

The heart rates of five weaned elephant seal pups were observed and measured at four stages during branding (Fig 2.5). There was a significant change in mean heart rate through the four stages of capture and branding ($F_{(2,3)} = 497.2$, $p = 0.002$). The mean heart rates of all the seals were significantly elevated upon restraint, increasing from 56 (± 5) to 148 (± 14) beats per minute (BPM) (Fig 2.5). There was no further increase in heart rate upon application of the hot brand – indeed, it decreased significantly ($t_4 = 3.9$, $p < 0.02$). The mean heart rate on restraint was 148 (± 14) BMP and 140 (± 10) BMP at branding. The mean heart rates of branded seals had returned to that rate measured prior to restraint and branding after ten minutes (Fig. 2.5).

Cryo-branding

Of the 50 seals cryo-branded in 1991, 26 were resighted in following years but could only be identified by their flipper tags. Of these 26 seals, 22 had been cryo-branded for 10 seconds and four for 30 seconds. Eighteen of these 26 surviving seals were resighted between January 1993 and March 2000. Eight were resighted in the year following branding.

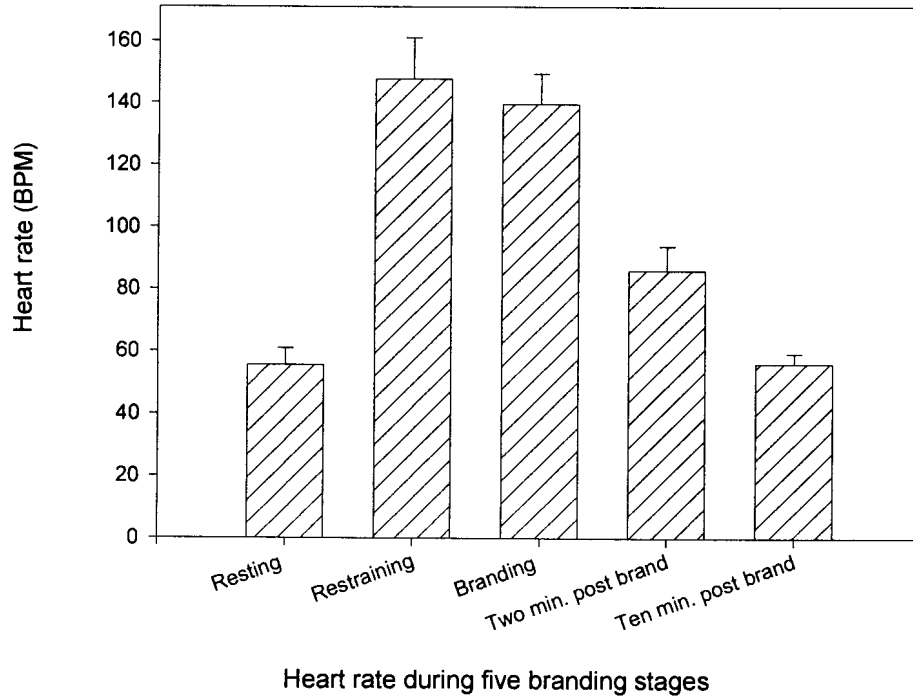


Figure 2.5. Heart rate (mean \pm SD) of five weaned elephant seals before, during and after branding at Macquarie Island. There was a significant change in heart rate through the four stages of capture and branding ($F_{(2,3)} = 497.2$, $p = 0.002$).

Discussion

Branding technique

Since the early branding studies at Macquarie Island (Chittleborough & Ealey 1951) the techniques have changed little. However, some procedures have been altered or added: (1) only seals with grey hair were branded i.e. fully moulted pups, (2) wounds in the brand area were avoided, (3) brand characteristics were monitored over time, and (4) survival of specific seal groups was assessed. The cast-iron branding irons were easy to heat using the gas furnace and they held their heat well while being transferred between the forge and seal. Using a gas furnace as opposed to the coke fired furnace allowed more rapid re-heating of brands and less work in maintaining the heat of the fire. Because hot iron branding is a swift method of marking animals, the seals only needed to be restrained for a short period (<60 s) to allow the application of a brand; and this was achievable by three persons. A further advantage of using the described technique and equipment in remote study areas is that LPG can be stored for long periods, unlike liquid nitrogen, and is relatively inexpensive.

There was heat loss of ~50-100 °C from the brands after they were used once and as they were transferred from one side of the seal to the other. The addition of one second to the application time on the second side to be branded produced good quality brand markings (Fig. 2.1) that were readable on both sides of the seal. Faint brand-marks were a consequence of shorter (2 vs. 3 second) application times. The trial of a two second brand application time on 2 000 seals in 1994 showed that this duration was barely sufficient (and sometimes not sufficient) to produce a permanent and clear marking. It appears that the two-second-application time failed to kill the all underlying melanocytes and hair follicles. Thus re-growth of hair over the brand scar occurred after the first moult (Mann & Heimbach 1995).

Three and four second branding produced sufficient heat to destroy the hair follicles and pigment-producing cells resulting in a clear tan coloured imprint on the skin (Chittleborough & Ealey 1951; Erickson *et al.* 1993; Merrick *et al.* 1996). A permanently bald and de-pigmented brand-mark (Chittleborough & Ealey 1951; Erickson *et al.* 1993; Merrick *et al.* 1996) persisted as a result of cell coagulation, necrosis and the denaturation of collagen in the dermis (Demling & Way 1991; Mann & Heimbach 1995).

Survival estimates and corrections

Southern elephant seals marked at Macquarie Island were recognised by both brands and tags. In the analysis above, seals were considered to have had “brand loss” if the brands on both flanks were unreadable. However this is a conservative approach (Burton, *personal communication*). In field practice, the observer will at times use a combination of brand characters from both flanks and thus reach an identity that would not have been possible from either brand alone. In addition to this, brand marks continue to improve with time, and thus once unreadable brands can become readable (Burton, *personal communication*).

Disregarding the extra determinations described above and just using individually assessed brands, the “maximum” estimate for “brand loss” was only 2.1%. As ~50% of all seals were both branded and double tagged, the estimate of “lost seals” can be approximately halved as they can be identified by tags. Thus the overall estimate of identity loss amongst all marked seals (both branded and tagged, and branded only) in the survivorship study is ~1%. However, the death of pups between birth and weaning (prior to marking) is ~5% (Antarctic Division records); and so the final adjustment to the first year survivorship estimate was to subtract 4%, and for all other years it was to add 1%.

Survival of the seals was unaffected by the trauma of branding. Survival rates to age one were almost the same for seals with unwounded brand-marks as for those with wounded brand-marks. The survival estimates for “tagged only” seals and branded seals were different however. Survival estimates for branded seals were higher in both of the years where concurrent marking programs occurred. These differences were due to the greater sightability of brands over tags as demonstrated by the higher recapture rates for branded seals and not due to the loss of tags as this factor was compensated for (Pistorius *et al.* 2000). However, it is important to note that the survivorship for branded seals was not less than that for tagged seals and hence branding certainly did not compromise survival. Indeed, branded California sea lions first-year pup survival was also not compromised nor was the condition of the seals, however only a few seals were branded (Aurioles & Sinsel 1988).

Brand-mark legibility

For all brandings prior to and after 1994 an application time of 3-4 seconds was used (Chittleborough & Ealey 1951). Most of the “brand-mark loss” category resulted from faint and unrecognisable brand-marks rather than unhealed, over-heated or smudged brand-marks.

Heart rates during branding

Heart rate measurements have been used as surrogates for stress responses and levels in free ranging animals (Ball & Amlander 1980; Culik *et al.* 1990; Giese 1998; Perry 1973). It is generally accepted that elevations in heart rate correspond to elevations in stress and that this response is gradient dependent (Culik *et al.* 1990; Giese 1998). Weaned pup heart rates were significantly higher when restrained compared to when they were being branded. Thus an elevation in heart rate cannot be attributed to the process of hot-iron branding itself; and it can be concluded that branding is no more stressful than capture. In studies of the behaviour of cattle that had been hot-iron and cryo-branded, it was handling *per se* that was responsible for any subsequent difficulties in handling the animals (Lay *et al.* 1992a; Lay *et al.* 1992b; Lay *et al.* 1992c; Schwartzkopf-Genswein *et al.* 1997). One possible reason that heart rate does not increase when brands are applied may be due in part to the cornified epidermal layer, the greatly thickened *stratum corneum* (Ling 1966; Ling 1967; Ling 1968) and thick blubber layer (Bryden 1964) that elephant seals have. It may be that the insulation these layers provide may protect the seals from the full heat stimulus of hot-iron branding. Increases in heart rate such as those observed when restraining seals are not uncommon in elephant seals since similar changes were observed (personal observation) when weaned pups were approached by larger male seals attempting to mate with them (Modig 1996; Wilkinson & van Aarde 1999).

Cryo-branding

Cryo-branding or freeze branding has been used at times to mark seals (Troy *et al.* 1997), and was trialled at Macquarie Island as an alternative to tagging and hot-iron branding. In this pilot study, seals that were cryo-branded were not identified in subsequent years from their brand-marks. All cryo-brand marks were lost after one year. The failure of the cryo-brands and the success of the hot-iron brands suggest that, for southern elephant seals at least, extreme heat is more effective at destroying melanocytes than extreme cold. This is probably because the demarcation of the necrosis zone (the brand mark) takes place during the first few days after branding (Knabl *et al.* 1999) and the consequences of hot branding are more acute and last longer than those of cryo-branding (Schwartzkopf-Genswein *et al.* 1997). It then follows that heat is more successful at destroying cells permanently and thus producing a clearly defined marking. Given the failure of the cryo-brand-marks in the present study and the mixed success of the technique experienced by other seal researchers (Merrick *et al.* 1996; Troy *et al.* 1997), it appears that cryo-branding is a generally less permanent technique for marking pinnipeds. This is likely to

be a result of the less complete killing of melanocytes achieved with cryo-branding (Schwartzkopf-Genswein *et al.* 1997) and thus the few killed melanocytes being replaced by ones peripheral to the branded site (Erickson *et al.* 1993; Merrick *et al.* 1996). This migration of cells does not appear to occur with hot-iron branding, probably because the central coagulation zone is so much larger (Mann & Heimbach 1995).

Cryo-brand-marks fade, need lengthy application times and thus long restraining times (Merrick *et al.* 1996). Even liquid nitrogen (when used as a coolant for brands) required 25 s to give good results with grey seals (Harkonen *et al.* 1999). In a study of cattle (Lay *et al.* 1992a; Lay *et al.* 1992b; Lay *et al.* 1992c) the prolonged restraint of the animal (required by cryo-branding) produced chronic stress. It must also be noted that it is not possible to assess the quality of the cryo-brands at the time of branding and to achieve a clear brand much experimentation is needed (Merrick *et al.* 1996; Troy *et al.* 1997). Clearly there are distinct advantages in reducing restraint and handling times of wild animals. There are also practical limitations to storing large volumes of liquid nitrogen for long periods under field conditions if large numbers of seals are to be branded. There do appear to be some species-specific differences. For example, fur seals retained cryo-brands better than elephant seals (Scheffer 1950) and harbour seals better than grey seals (Harkonen *et al.* 1999).

Thus freeze-branding of seals has delivered uncertain results to date as Erickson *et al.* (1993) remarked, “seal researchers have experienced mixed success and many investigators have abandoned the procedure”. The main problem had been the loss of the marks over time (several years) as no ill-effects on the seals have been reported (Troy *et al.* 1997). Troy *et al.* (1997) hot-iron branded some New Zealand fur seal (*Arctocephalus forsteri*) individuals after their freeze-brands were lost following melanocyte regrowth. Two of ten of her hot-iron branded seals had infections of the brand site visible within the first six months but all were healed after 12 months. By contrast, Harkonen *et al.* (2001) report no problems with the long-term (up to 14 years) re-sightings of harbour seal (*Phoca vitulina*) individuals cryo-branded on the west coast of Sweden (Harkonen & Harding 2001) and reported that brand marks could be seen up to 500 m distant (Harkonen *et al.* 1999).

Conclusions

As a means of giving individually characteristic marks to elephant seals for their whole lives, hot-iron branding has much merit. It is a swift procedure that does not appear to disturb the seal any

more than the capture process itself. This was clearly demonstrated by the measurements of the heart rate of seals during hot iron branding in this study. First year survival of seals was not adversely affected regardless of brand quality. Brand-marks are clear “one-time” marks that grow with the seal’s skin. There is nothing in or on a brand-mark that can catch or tear as there is in a tag with its attachment hole. Tags are prone to being caught on rocks or under other seals and to abrade or tear the surrounding flesh (Bradshaw *et al.* 2000; Pistorius *et al.* 2000; Testa & Rothery 1992a; Wilkinson & Bester 1997) and biofouling is common (Schmidt 1998). In my experience, brand-marks are more easily read from afar and thus disturbance to the seals is kept to a minimum, whereas seals that are flipper tagged are often disturbed when their flippers, which regularly lay together and obscure tags, have to be moved. Flipper tags also need to be read at a closer range. These constraints also apply to PIT tags.

Hot-iron branding is the most appropriate marking technique tested at Macquarie Island and was considered a swift means of permanently and uniquely identifying individual seals in the field over long periods. However, as noted previously (Erickson *et al.* 1993) there is not consensus on the use of hot branding within the scientific community.

Chapter 3 - Invasive Research Methods in Wildlife Research: Impacts at the Population Level

Introduction

Global management of wildlife is best underpinned by an unbiased (scientific) understanding of the basic biology of the species at issue. Historically, wildlife research has been directed at gathering knowledge about individual species; but recently research attention has focussed more on investigating and understanding the habitat and conservation requirements of species with decreasing or vulnerable populations (Reijnders *et al.* 1993). This includes species such as the southern elephant seal. Wildlife research has already been directed to devising practical methods to conserve some species in Antarctica (Anderson *et al.* 1991).

Research, which is directed at determining ecological interactions and the relatedness of species, may require the use of invasive methods (Farnsworth & Rosovsky 1993). These include implanting transmitters, taking blood, applying chemical anaesthesia and using manual restraint of the subjects (Grigg 1999). Thus much of the research conducted in Antarctica, as elsewhere, is subject to approval from various ethical bodies that assess and balance the impacts of the research against the benefits (Bateson 1991; Cuthill 1991; Farnsworth & Rosovsky 1993). But, little is known about the Antarctic environment (Anderson *et al.* 1991) and indeed the impact of research activities to date (Hofer & East 1998).

Assessing the impact of human research activities on wildlife is therefore vital to the ethics debate and thus necessary for sound ecosystem management. The impact of anthropogenic disturbance (e.g. research and tourism) on free-living animals in Antarctica has become a focus of recent studies (Culik & Wilson 1991; Culik & Wilson 1995; Engelhard *et al.* 2001; Galimberti *et al.* 2002; Giese 1998; Nimon *et al.* 1995). This has occurred out of concern for animal welfare generated by increasing biological research and Antarctic tourism (Anderson *et al.* 1991; IAATO 2001). The southern elephant seal, for example, has been described as one of the most widely and exhaustively studied of all pinnipeds (Ling & Bryden 1992) yet there is much more to be known (Burton & van den Hoff 2002) of the effect of human activities on this species and of almost all (sub-) Antarctic pinnipeds and seabirds. Clearly there is room for research that contributes to the debate regarding animal welfare, research, conservation and ethical considerations.

Research techniques such as handling, tagging and anaesthesia are considered invasive and have been shown to have some detrimental effects on survival for some species (Hofer & East 1998).

Although no adverse effects to research and disturbance have been documented in elephant seals (Engelhard *et al.* 2002; Engelhard *et al.* 2001), several other marine mammal studies have shown short-term adverse changes in behaviour and physiology resulting from human activity (Born *et al.* 1999; Engelhard *et al.* 2001; Reijnders *et al.* 1993; Suryan & Harvey 1999). However, no pinniped studies have assessed the impact of research disturbance in terms of a longer-term fitness parameter such as survival. As part of a demographic study to discover the cause(s) of the decrease in the population of southern elephant seals (*Mirounga leonina*) at Macquarie Island I: (1) assessed the size and body composition of seal pups at birth and at weaning, (2) permanently marked the pups and (3) followed them through their lives.

In addition, data related to repeated handling and to the future survival of elephant seal pups was studied. Specifically, the effect of multiple captures for life history and ecologically related studies on the prospects of first year survival was assessed. This is the first time the effect of human disturbance has been quantified with respect to the first year survival of an endangered (in Antarctica) marine mammal.

Methods

Southern elephant seals were captured at Macquarie Island in 1998 as part of a long-term demographic study to collect life history information. Seals were exposed to varying degrees of handling during the period from their birth, through weaning to their first foraging trip departure and beyond. There were two study groups: a single capture group and an intensively studied group which involved multiple captures.

Single capture group

A group of 100 weaned pups were caught once, permanently marked (branded) and released.

Intensive captures group

First handling: Five hundred pups were caught at birth, weighed and marked with two individual flipper tags for identification. The time taken for this procedure was between 2 and 3 minutes.

Second handling: The same seals were recaptured 24 days later at weaning and morphometric measurements taken (McMahon *et al.* 1997). Two to three minutes were required to complete these measurements.

Third handling: After a further three to four weeks the same pups were recaptured and permanently marked (branded) within a minute (McMahon *et al.* 1997).

Further handling: One hundred of the already handled and marked pups were randomly selected and caught twice after weaning to assess body composition using total body water techniques (Anderson & Fedak 1987; Fedak & Anderson 1982) before they went to sea for their first foraging trip.

Thus a series of pre-departure capture histories were available for each seal with the minimum number of captures being one and the maximum being five.

Juvenile elephant seals usually return to their natal islands twice in their first year: once during the mid-year haulout (aged approximately six months) and again for their first moult (aged 13 months) (Hindell & Burton 1988b). Forty-five of the intensively studied seals were recaptured at these times to assess growth parameters. These mid-year haulout captures were added to the pre-departure captures and in so doing, the total number of captures was assessed in the survival model.

Capture-history matrices were constructed from the resight history of individually marked seals. The matrices were used as input files for the capture-mark-recapture (CMR) program MARK (White & Burnham 1999) to estimate capture probabilities and survival of the study population. MARK provides survival (ϕ) and recapture (ρ) estimates under the Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965) and under several models that appear as special cases of the CJS-model (Lebreton *et al.* 1992).

Individual covariates of survival were included in the model by expressing the natural logarithm of the probability of survival, i.e. the logit of survival, as a logistic function of the covariates:

$$\text{Logit}(\phi) = y \text{ intercept} + \beta_{(x)} \left(\frac{x - \bar{x}}{SDx} \right) - \beta_{(x^2)} - \left(\frac{x^2 - \bar{x}^2}{SDx^2} \right) \quad \text{Equation 1}$$

Where Logit (ϕ) is the survival estimate of a seal with the covariate x , β is the logit function parameter calculated in MARK for covariate x and SD is the standard deviation of the covariate x . This model (function) is embedded in the log-likelihood function for survival as in a logistic regression. This model assumes that there is an optimal value for the variable x and that there are some selective penalties associated with the extreme values of x .

Starting from a general model which fits the data, the Akaike information criteria scores (AIC) and Δ AIC scores were used to select the most parsimonious model(s) (Burnham & Anderson 2001) and likelihood ratio tests within MARK were used to test specific hypotheses (Lebreton *et al.* 1992). As a rough guide Burnham & Anderson (2001) suggest that models with Δ AICs ≤ 2 have substantial support, those with Δ AICs of 4-7 have some support while those models with Δ AICs > 10 have no support. Likelihood-ratio tests (LRT) programme MARK were used to test for specific differences between groups.

Results

The mean estimate for first year survival (corrected for brand-loss as described in Chapter 2) was $74.35 \pm 2.34\%$. The inclusion of a gender (g) component to the general survival model did not improve model performance and accordingly it was concluded that first year survival estimates were unaffected by seal gender ($\chi_1^2 = 0.627$, $p = 0.43$) (Table 3.1).

Table 3.1. Akaike information criteria (AIC), delta AIC (Δ AIC), Akaike weights, number of parameters and the deviance for the candidate survival (ϕ) and recapture (ρ) models. The covariates are as follows: birth mass (b), wean mass (w), pre-departure captures (p), post-departure captures (s), total number of captures in the first year of life (f) and age-based (a) rather than time-based (t) survival.

Model	AIC	Δ AIC	AIC-weight	Parameters	Deviance
$\phi(a, b, w, p, s, f) \rho(c)$	1792.542	0.0	0.54506	12	1768.27
$\phi(a, b, w, p, s, f) \rho(t)$	1792.906	0.36	0.45436	13	1766.58
$\phi(a, b, w, s, f) \rho(t)$	1806.253	13.35	0.00057	14	1777.88
$\phi(a, b, p, s, f) \rho(t)$	1824.121	31.22	0	11	1801.89
$\phi(a) \rho(c)$	1870.990	78.08	0	3	1864.97
$\phi(a) \rho(t)$	1873.004	80.1	0	4	1864.97
$\phi(a, g) \rho(t)$	1874.395	81.49	0	5	1864.34
$\phi(t) \rho(t)$	1875.834	82.93	0	6	1863.76

Annual seal recapture probabilities were similar in the years of recaptures and did not affect survival estimates ($p \gg 0.05$, $\chi_1^2 = 0.00$) because the model that included constant recaptures ($\rho(c)$) performed as well as the model that included variable annual recapture rates ($\rho(t)$). First

year survival in elephant seals was unaffected by capture frequency during the first weeks and first year of life (Fig.3.1), however, wean mass was a significant determinant of first year survival ($p < 0.01$) explaining 76% of the observed variability in survival (Fig.3.2). The survival estimate for seals captured only once during the pre-departure phase was 0.7930 (95% CI 0.6945, 0.860), for seals captured twice it was 0.6446 (95% CI 0.4261, 0.8159), for seals captured three times it was 0.7191 (95% CI 0.6576, 0.7733), and for seals capture four times it was 0.8253 (95% CI 0.7120, 0.9003). Similarly the survival estimates for the total numbers of captures was **0.7930** (95% CI 0.6945, 0.860), **0.6429** (95% CI 0.4290, 0.8131), **0.7093**, (95% CI 0.6463, 0.7651), **0.8253**, (95% CI 0.7120, 0.9003) and **0.9750** (95% CI 0.8427, 0.9965) for seals captured once, twice, three-, four- and five times respectively. Capture frequency prior to the seal's first departure to sea was unrelated to survival (LRT $p = 0.6$) as was the total capture frequency during the first year of life (LRT, $p = 0.19$).

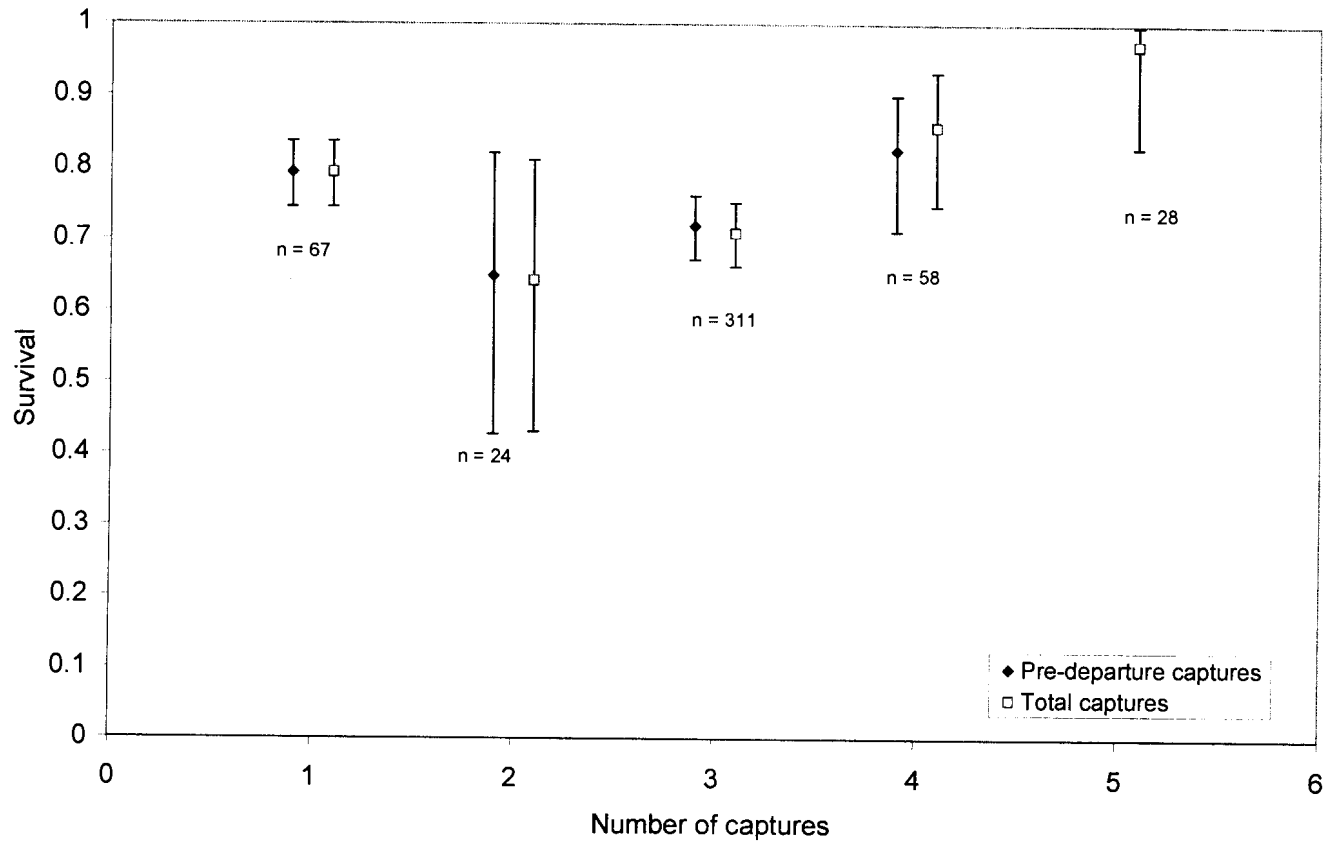


Figure 3.1. Mean \pm 95% confidence intervals of first year survivorship for singly and multiply captured elephant seal pups. The total captures are a combination of pre-departure and return captures.

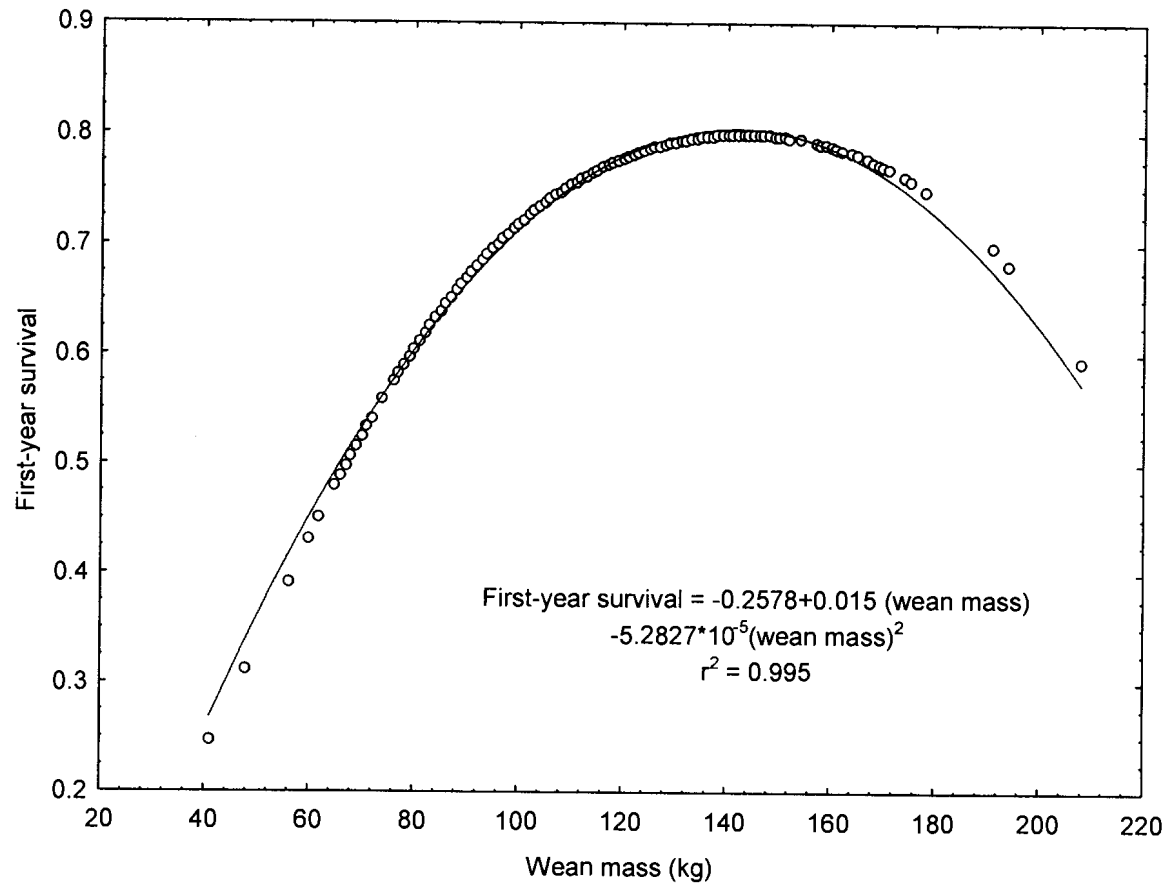


Figure 3.2. The non-linear relationship between wean mass (kg) and first year survival of elephant seal pups from Macquarie Island showing that first year survival is largely (99.5%) explained by the variation in mass at weaning.

Discussion

This study provides data which measures the effect of repeated handling by researchers of free living seals. The survival of pups to age one was unaffected by repeated handling and the use of invasive research methods such as anaesthesia and instrument deployment during the first weeks of life. This is the first such study to assess research disturbance during a critical early phase of a large mammal's life and which relates this to the ultimate survival of an individual. Other studies have assessed the effects of anthropogenic disturbance in the immediate to short-term (hours, days) (Ardern *et al.* 1994; Hofer & East 1998), but did not relate anthropogenic disturbance in the longer term (months, years). However, a study (Ginsberg *et al.* 1995) of wild dogs (*Lycaon pictus*) and another of cheetahs (*Acinonyx jubatus*) (Laurenson & Caro 1994) have examined the consequences of handling on survival and found that survival was not influenced by research handling. There have been two studies to date of Antarctic predators, which have assessed the influence of anthropogenic (research and tourist) disturbance on wildlife populations. The first has been of the southern elephant seal (Wilkinson & Bester 1988) and the second of the Adélie penguin, (Culik & Wilson 1991; Culik & Wilson 1995; Fraser & Patterson 1997; Nimon *et al.* 1995). The results of these studies were ambiguous as some (Culik & Wilson 1991; Culik & Wilson 1995) showed a negative outcome while others (Fraser & Patterson 1997; Nimon *et al.* 1995; Wilkinson & Bester 1988) found no effect. However, neither assessed the consequences of handling against the future survival of individual animals.

McMahon *et al.* (2000) have previously shown that elephant seal pups are reliant on the fat stores accumulated during the first weeks of life for first year survival. I hypothesised that repeated handling during lactation and beyond might influence the accumulation, assimilation and availability of the pup's vital fat reserves by: (1) decreasing the suckling time when disrupting the mother-pup bond, (2) increasing metabolic rates such that valuable resources are prematurely utilized and not available during the first foraging trip and (3) altering physiological states such as immuno-responses. None of these negative factors appear to have occurred because repeated captures of elephant seal pups between birth and the post weaning fast did not affect individual survival probability.

Thus invasive research during the lactation and the post weaning fast of southern elephant seals has neither a short-term effect (Engelhard *et al.* 2001) nor a long-term effect that compromises survival (this study). Elephant seals are therefore capable of dealing with invasive research and considerable interaction with humans during their early life stages. One possible reason is their

natural context when young. They may be pre-adapted to disturbance early in life because of the disruptive and often hazardous nature of their breeding harem environment (Galimberti *et al.* 2000a; LeBoeuf & Mesnick 1990; McCann 1981; McCann 1982). They also often experience antagonistic behaviour in moult wallows after weaning.

But what of animals that have not been handled? Survival of unmarked and thus unhandled seals cannot be determined (Caughley 1977; Seber 1973). To compensate for this the probability of survival was related to a gradient dependent variable (handling). I assumed a decreased survival probability with increased handling frequency, because in penguins (Culik *et al.* 1990) it was found that anthropogenic disturbance resulted in a gradient dependent stress and heart rate response. In the absence of such a gradient dependent response in elephant seal pups, it was concluded that handling does not affect first year survival and that handled seals have similar survival probabilities to non-handled animals.

Survival is a fundamental and determining component of population size (Caughley 1977). Therefore, in the absence of any increased mortality in response to additional episodes of invasive research disturbance, it follows that elephant seal populations are unlikely to be affected by human research activities. This may also apply to other communal-breeding seal populations.

In conclusion, it cannot be assumed that anthropogenic (wildlife research) disturbance, even at a critical phase in the life cycle of an animal, will necessarily compromise individual and population fitness. Indeed there has been an instance where it was hypothesized that handling of wild animals caused direct harm to their survival (Burrows 1992). It was suggested that wild dogs had become locally extinct due to handling (Burrows 1992). However, after a thorough analysis of the effects of handling on wild dogs, no evidence could be found that handling was associated causally with increased mortality (Ginsberg *et al.* 1995). As different species do not respond to handling in the same way (Hofer & East 1998), it would seem prudent that some species-specific preliminary research be conducted to determine the effects of handling when new studies are initiated.

The concern that human disturbance (tourism) and wildlife research may impact adversely on Antarctic wildlife may be justified for some kinds of human disturbance. But the data presented here suggest that potentially adverse outcomes of some research activities can be negligible relative to the effects imposed by the environment itself. Nonetheless, ethical considerations suggest that researchers working with animals (in this case southern elephant seals) limit the

research and procedures to those that have been proven safe (Farnsworth & Rosovsky 1993). However such information is not always available and therefore studies such as this and others (Ginsberg *et al.* 1995) offer a valuable contribution. This is because they provide information on an important life history parameter that can be measured and compared to that of other wild animals. Also, studies such as these above (and this study) provide quantitative information that may be directly applicable to closely related species for which data on handling effects are not available.

Chapter 4 - A demographic comparison of two southern elephant seal populations

Introduction

Southern elephant seals (*Mirounga leonina*, Linnaeus 1758) have a circumpolar distribution and four distinct population stocks are recognized: the Peninsula Valdés stock in Argentina, the South Georgia stock in the South Atlantic Ocean, the Kerguelén stock in the south Indian Ocean and the Macquarie stock in the southern Pacific Ocean (Hoelzel *et al.* 2001; Slade *et al.* 1998). The principal breeding colonies are located at: Peninsula Valdés, South Georgia Island, Heard Island, Îles Kerguelén and Macquarie Island. Overall, the southern Pacific and southern Indian Ocean southern elephant seal populations have decreased over the last few decades (Barrat & Mougin 1978; Burton 1986; Condy 1978; Guinet *et al.* 1992; Hindell 1991; Hindell & Burton 1987; Pistorius *et al.* 1999b). Recently the decrease at Îles Kerguelén was believed to have reversed (Guinet *et al.* 1999), and to have stabilized at Heard Island (Slip & Burton 1999) and Marion Island (Pistorius *et al.* 2001), but continues at Macquarie Island (Hindell *et al.* 1994b). The southern Atlantic Ocean populations at South Georgia, the Falkland Islands and Peninsula Valdés have remained stable or increased (Boyd *et al.* 1996; Campagna *et al.* 1993; Galimberti & Boitani 1999), with only the very small population at Gough Island showing a long-term decrease (Bester *et al.* 2001). The cause(s) for the decrease in the southern Pacific Ocean population remain(s) unknown, although it may be similar to that at Marion Island where food limitation has been implicated (Pistorius *et al.* 1999b). Long-term mark-recapture studies were established at Macquarie Island (McMahon *et al.* 1999) and at Marion Island (Bester 1988; Pistorius *et al.* 1999a; Pistorius *et al.* 1999b) to address the proximate causes of the observed decreases. In both studies, elephant seals were marked and followed by subsequent recaptures, to determine age-specific survival.

Survival (or mortality) is probably the most useful demographic parameter that enables ecologists to interpret and understand animal population dynamics for fundamental and applied purposes (Lebreton *et al.* 1992; Lebreton *et al.* 1993). Survival is important because changes in survival are often associated with changes in population structure and size (Lebreton *et al.* 1993; Smith & Fowler 1987). Age-specific survival estimates are especially important (Caughley 1977). To determine age-specific survival, animals need to be permanently and individually marked, or marked in a fashion that allows for compensation of lost marks, and then followed throughout their lives (Caughley 1977). This requires long-term monitoring of the population and a method of marking animals that essentially is permanent, legible and has no mortality effects.

Permanent emigrations from a birth site where animals are marked are important behavioural traits when estimating survival rates because animals that do not return to their natal sites are not available for recapture (Caughley 1977). Emigration from a Capture-Mark-Recapture study site therefore compromises survival through wrongly assigning live animals to a dead class through non-capture (Caughley 1977; Lebreton *et al.* 1993). There is little permanent migration of elephant seals to and from Macquarie Island and Marion Island (Bester 1988; Condy 1978; Hindell & McMahon 2000; Nicholls 1970; Slade *et al.* 1998). Slade *et al.* (1998) estimate exchange to be approximately $1 \cdot 10^{-5}$ females per generation between most populations. I assumed therefore that loss of seals through migration to be negligible.

By studying two populations, one that continues to decrease (Macquarie) and one that has possibly stabilized (Marion), I aim to identify characteristics of both populations as a means of elucidating the causal parameters that may be driving/ have driven the population decreases. To achieve this I:

1. Assess the concurrent age-, sex- and cohort specific survival of the two populations.
2. Determine the mean wean masses of seals at each location as a proxy measure of maternal foraging success and prey availability.
3. Calculate the mean age at first breeding for each site.
4. Propose a hypothesis that describes the causal factors driving elephant seal decreases.

Methods

Marking and resighting at Macquarie Island

At Macquarie Island 4 322 recently-weaned and tagged southern elephant seal pups were captured and branded from 1993 through 1997 on the isthmus (54° 30' S, 158° 50' E). Fifty millimetre cast-iron cattle brands were used to hot brand seals on both rear flanks (Carrick & Ingham 1960; Carrick & Ingham 1962a; Chittleborough & Ealey 1951). A four-character alphanumeric brand consisting of a letter prefix followed by a three-digit number uniquely identified the cohort and the individual respectively. All 4 322 branded seals were tagged at birth in the inter-digital webbing of their hind flippers with two uniquely numbered plastic tags (McMahon *et al.* 1997).

Daily searches of the isthmus beaches and tussock areas and monthly searches of the entire island beaches and tussock areas were made to resight (recapture) marked seals from 1994-2001. At the time of resighting, location on the island, sex, brand number, tag numbers and the number of tags present were recorded. Both brands and tags were read. Flipper tags were used to validate brand identifications and *vice versa*.

Marking and resighting at Marion Island

At Marion Island (46° 54' S, 37° 45' E), 2 056 recently weaned seals were individually marked with two uniquely numbered and colour-coded plastic tags in their hind flippers from 1993-1997 (Pistorius *et al.* 1999a; Pistorius *et al.* 2000). Beaches occupied by elephant seals were searched every 10 days from 1994 to 2000 except for the breeding seasons when they were searched every seven days (Pistorius *et al.* 2000). The seal marking and resighting techniques used at Marion Island are reported in full elsewhere (Pistorius *et al.* 1999a; Pistorius *et al.* 2000). They differ from those at Macquarie Island only in that tags are applied at weaning and not at birth. Cumulative age-specific tag retention rates, estimated from double-tagged individuals (Pistorius *et al.* 2000), were used to adjust the survival estimates to compensate for tag loss.

Wean mass measurements

A total of 4 322 pups were flipper tagged at birth and weighed (± 1 kg) on the day of weaning at Macquarie Island (McMahon *et al.* 1997). Some 335 pups at Marion Island were marked on the day of weaning and were weighed (± 1 kg) shortly (0-22 days) thereafter; and their reconstituted weaning masses calculated following (Wilkinson & Bester 1990). Wean masses were collected between 1993 and 1997 at each island. These wean masses were compared to those presented by (Burton *et al.* 1997). The wean masses were included as individual covariates in the mark-recapture model, to assess the influence of maternal investment on age-specific survival because it is known that wean mass acts as a proxy for maternal investment (Arnbom *et al.* 1997; Fedak *et al.* 1996) and probably prey availability as well (Burton *et al.* 1997).

Individual covariates of survival such as wean mass were included in the survival model by expressing the natural logarithm of the probability of survival, i.e. the logit of survival, as a logistic function of the covariates:

$$\text{Logit}(\phi) = \text{y-intercept} + \beta_{(x)} \left(\frac{x - \bar{x}}{SDx} \right) - \beta_{(x^2)} - \left(\frac{x^2 - \bar{x}^2}{SDx^2} \right) \quad \text{Equation 1}$$

Where Logit (ϕ) is the survival estimate of a seal with the covariate x , β is the logit function parameter calculated in MARK for covariate x and SD is the standard deviation of the covariate x . This model (function) is embedded in the log-likelihood function for survival as in a logistic regression. This model assumes that there is an optimal value for the variable x and that there are some selective penalties associated with the extreme values of x .

Mark-recapture analysis

Capture-history matrices were constructed from the resight histories of individual seals. Multiple resights within a year were treated as a single sighting. These capture matrices were used as input files for the capture-mark-recapture (CMR) program MARK (White & Burnham 1999) to estimate survival and capture probabilities after weaning. MARK provides survival (ϕ) and recapture (p) estimates under the Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965) and under several models that appear as special cases of the CJS-model (Lebreton *et al.* 1992).

Parametric Goodness-of-fit (GOF) tests within MARK were used to test whether the CJS-model assumptions were met (Burnham *et al.* 1987; Lebreton *et al.* 1992). This bootstrap procedure simulates encounter histories that exactly meet the CJS-model assumptions. These simulated data are compared to the field data for compliance with the CJS-model assumptions (White & Burnham 1999). Test 2 and Test 3 in programme Release (which is included in programme MARK) also provide GOF statistics. Test 2 deals animals known to be alive and tests whether all animals have the same capture probabilities while Test 3 tests whether all seals have the same probability of survival. Thus these test provide valuable information of the behaviour of the study animals. To test the main hypothesis (e.g. affect of sex, age, and cohort on survival) the chi-square (χ^2) Likelihood-Ratio-Test (LRT) statistics within program MARK were used (Lebreton *et al.* 1992; White & Burnham 1999).

Mean age of primiparity and net reproductive ratio

The mean ages at which females gave birth for the first time (primiparity), at Macquarie Island and at Marion Island, were calculated using the model described by deMaster (1981). This model calculates the probability of a female giving birth at a particular age from the number of females seen with young and the total number of females seen in that age class as follows:

$$\hat{Y}(x) = \frac{l(x)}{n(x)}$$

Where x = the age of the female

$\hat{Y}(x)$ = the estimated proportion of reproductive females at age x

$T(x)$ = the number of females at age x with pups or who are pregnant

$N(x)$ = the total number of females observed (alive) at age x

Therefore the probability of giving birth before age x , $Z(x)$ is:

$$Z(x) = \hat{Y}(x) [1 - \hat{Y}(x)] * Z(x-1)$$

The probability of giving birth for the first time age age x , $r(x)$ and the probability of giving birth at or before age $x-1$, $Z(x-1)$, equals $Z(x)$. The probability of reproducing for the first time at age x is therefore:

$$R(x) = Z(x) - [Z(x)-1]$$

And the average age at first birth, $B(x)$, is therefore:

$$B(x) = \sum_{x=0}^w x * r(x)$$

Where w is the minimum age where $Z(x) = 1.0$

Because breeding and moulting occur at different times and not all females alive haul out during the breeding season (Carrick *et al.* 1962b), the total number of seals known to be alive at that age was used to represent the total number of females in that age class, and all females hauling out during the breeding season were assumed to give birth (Pistorius *et al.* 2001).

The rate of increase R_0

An often used population fitness measure is the per generation ratio of increase (multiplication), R_0 , that is defined as follows:

$$R_0 = \sum l_x * m_x \quad \text{Equation 2}$$

Where l_x is the proportion of individuals that survive from birth to age x , and m_x is the average number of female offspring produced by a female at age x . This ratio of multiplication was calculated for each island population up to and including females aged 10 years.

Results

Goodness of fit

The parametric GOF bootstrap (MARK) results for both the Macquarie Island and Marion Island data sets show significant ($p < 0.0001$) departures from the CJS-model assumptions. The overall data sets were further analysed using program RELEASE to explicate the causes for the observed lack of fit (Burnham *et al.* 1987). The sum of the overall, male and female Macquarie Island seals, χ^2 -value for Test 2 was 746.8670 (df = 20) $p < 0.0001$ indicating variation in recapture rates of seals. The overall χ^2 -value for Test 3 was 334.3020 (df = 16) $p < 0.0001$ which is indicative of variation in survival. Similar results demonstrating heterogeneous recapture and survival rates were obtained for the Marion Island population, the overall Test 2 χ^2 -value was 568.1 (df = 10) $p < 0.0001$ and the overall Test 3 χ^2 -value was 315.1 (df = 18) $p < 0.0001$. However, because heterogeneity in capture probabilities (departure from the CJS-model assumptions) have been shown not to substantially affect survival rate estimates (Barker 1992; Nichols *et al.* 1982; Pollock & Raveling 1982) I present survival estimates as those calculated from program MARK.

Recaptures

The most parsimonious models for the Macquarie Island and Marion Island data sets were those that incorporated age and cohort based survival components and time and age based recapture components (Table 4.1). Recapture probability varied significantly between years at both Macquarie Island ($\chi^2_5 = 201.3$, $p < 0.0001$) and at Marion Island ($\chi^2_5 = 185.8$, $p < 0.0001$) (Fig. 4.1). The recapture probabilities of marked seals at Marion Island were significantly ($\chi^2_6 = 376.5$, $p < 0.0001$) higher than those recorded at Macquarie Island (Fig. 4.1).

At Macquarie Island survival estimates for all years, except the third year, were higher than at Marion Island (Fig. 4.2). Significant ($\chi^2_5 = 22.26$, $p < 0.0005$) differences were evident in the age specific survival estimates of seals at Macquarie and Marion islands (Fig. 4.3). The most notable differences between the populations occurred in the first, second and fifth and sixth years of life. The inclusion of a gender element in the recapture component did not improve the model significantly ($\chi^2_{15} = 24.12$, $p = 0.063$). However, gender significantly ($\chi^2_{20} = 48.55$, $p = 0.0004$) affected the survival estimates at Macquarie Island and at Marion Island ($\chi^2_{20} = 32.29$, $p =$

Table 4.1. Selection of the most parsimonious models for the Macquarie and Marion Island data sets under the full CJS-model for estimating survival in elephant seals. For each model the Akaike Information Criterion (AIC), number of estimable parameters

Model	AIC	Δ AIC	AIC Weight	NP	Deviance
ϕ (age, island group, log (wean mass) ages 1-2 at MQ, linear (wean mass) age 1 at MR) ρ (island group, time)	29093.90	0	0.60	31	29031.75
ϕ (age, island group, log (wean mass),ages 1-2 at MQ and age 1 at MR) ρ (island group, time)	29094.73	0.84	0.39	32	29030.59
ϕ (age, island group, log (wean mass) at MQ and linear (wean mass) at MR) ρ (island group, time)	29102.20	8.3	0.01	44	29013.94
ϕ (age, island group, log (wean mass)) ρ (island group, time)	29104.67	10.8	<0.01	48	29008.34
ϕ (age, log (wean mass) ρ (island group, time)	29111.16	17.4	<0.01	32	29047.01
ϕ (age, island group, log (wean mass),ages 1 MQ, ages 1 MR) ρ (island group, time)	29131.26	36.4	0	30	29071.13
ϕ (age, island group, linear (wean mass),ages 1-2 MQ, ages 1 MR) ρ (island group, time)	29163.15	69.3	0	29	29105.03
ϕ (age, linear (wean mass)) ρ (island group, time)	29175.62	81.7	0	26	29123.52
ϕ (age, island group) ρ (island group, time)	29350.84	256	0	26	29298.74
ϕ (age) ρ (island group, time)	29361.9	267	0	20	29321.84
ϕ (age) ρ (time)	29405.51	324	0	19	29367.46
ϕ (time, island group) ρ (island group, time)	29444.40	350	0	27	29390.30

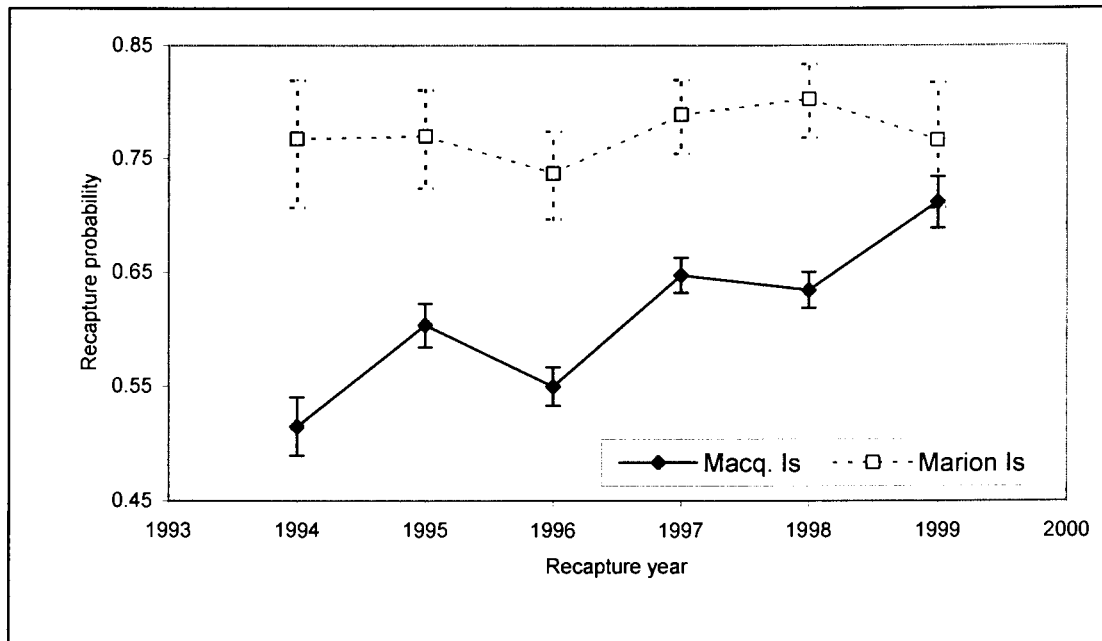


Figure 4.1. The recapture probability estimates ($\pm 95\%$ confidence limits) of southern elephant seals for Macquarie (solid line) and Marion (dashed line) islands. The recapture rates were calculated in program MARK and represent the total recapture estimates for all cohorts and ages in that whole year.

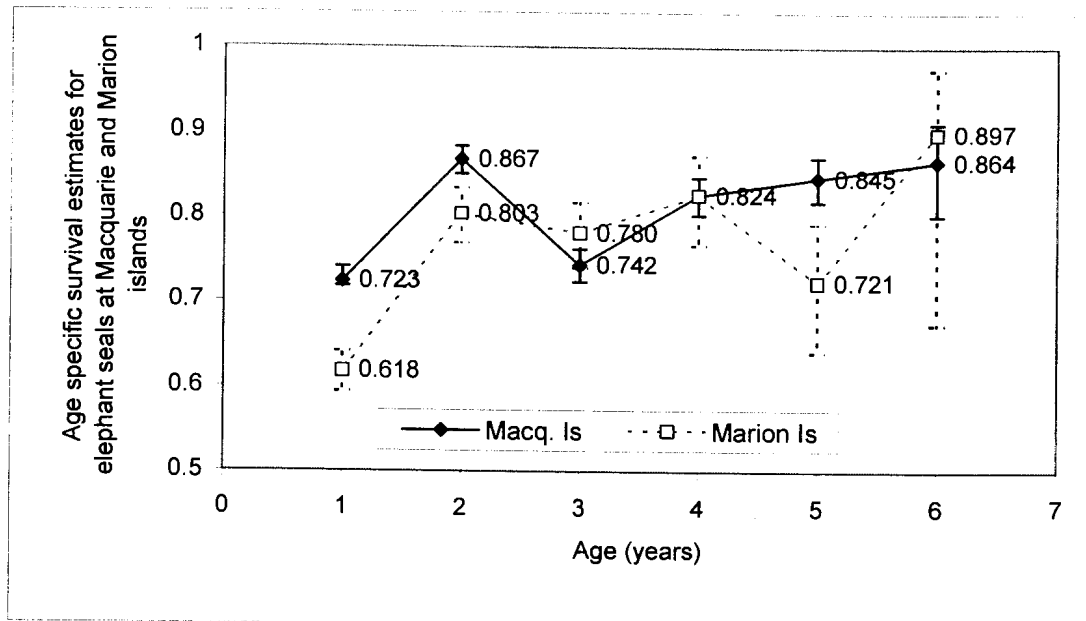


Figure 4.2. The age specific survival rate estimates ($\pm 95\%$ confidence limits) for southern elephant seals at Macquarie (solid line) and Marion (dashed line) islands. The survival estimates are for male and female seals combined.

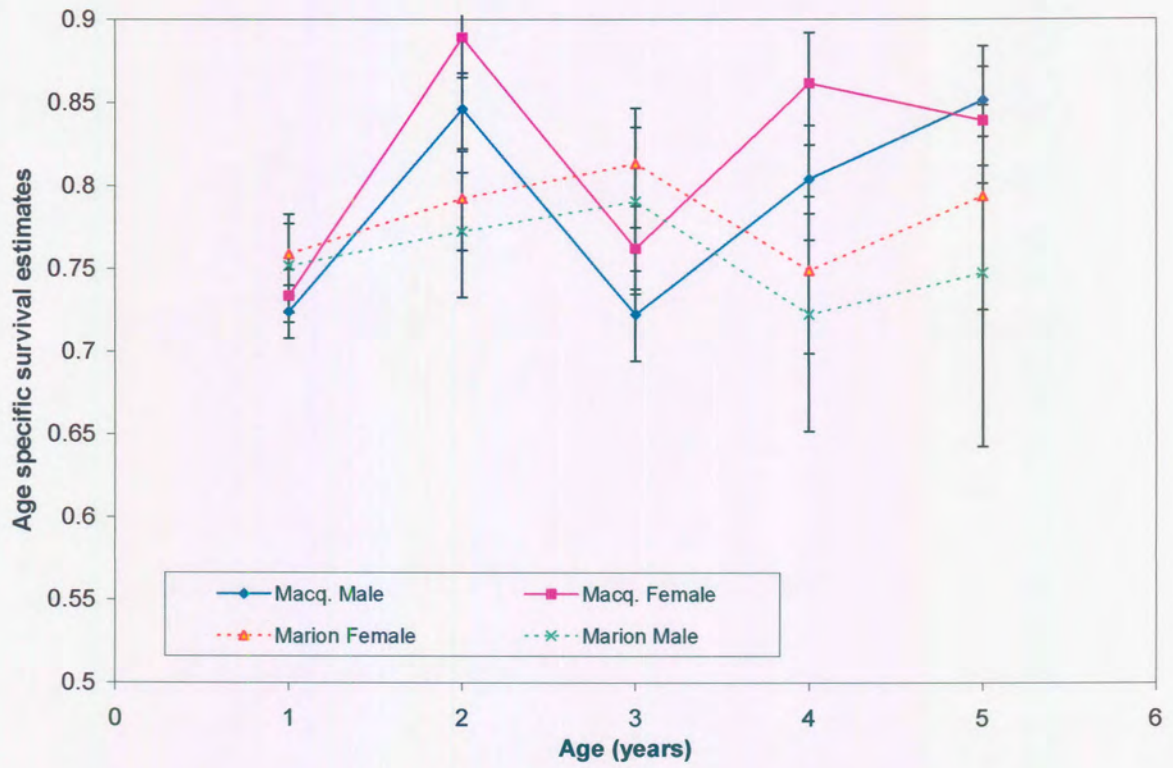


Figure 4.3. The age specific survival rate estimates ($\pm 95\%$ confidence limits) for southern elephant seals at Macquarie (solid line) and Marion (dashed line) islands.

0.0403). Female seals at both locations had consistently higher survival rates than male seals (Fig. 4.3).

Age-specific survival estimates at Macquarie and Marion islands

Overall age specific survival for male seals at Macquarie Island differed significantly from that for males at Marion Island ($\chi^2_6 = 24.46$, $p = 0.0004$), the most notable differences occurring during the first year of life (Fig.4.3). Similarly for females, overall age specific survival differed between the islands ($\chi^2_6 = 34.37$, $p < 0.0001$) and the major differences again occurred in the first and second years of life (Fig. 4.3).

The mean first year survival estimate for five successive cohorts at Marion Island was significantly ($Z_5 = -3.87$, $p < 0.001$) less than for concurrent cohorts at Macquarie Island (Fig. 4.4a, 4.4b & 4.4c). The variance in first year survival for the five Marion Island cohorts was 0.0045, while it was 0.0009 for the five Macquarie Island cohorts. Age specific survival estimates for male and female seals were significantly different at both Macquarie Island ($\chi^2_6 = 34.66$, $p < 0.0001$) and at Marion Island ($\chi^2_6 = 20.37$, $p = 0.002$). Female survival estimates were consistently higher than male survival estimates. However, inclusion of seal-sex did not contribute significantly to model performance when wean mass was included in the models neither for Macquarie Island seals ($\chi^2_{10} = 11.59$, $p = 0.31$) nor Marion Island seals ($\chi^2_8 = 4.54$, $p = 0.81$). Thus, male and female seals were pooled in the age-specific survival analysis in order to assess the impact of wean mass.

Wean mass and survival

The mean wean masses of male and female seals combined from 1993-1997 were not significantly different between islands ($T_{6837} = 1.169$, $p = 0.242$). At Macquarie Island the mean wean mass was 118.8 kg (SD = 27.2, $n = 6504$) while at Marion Island the mean wean mass was 120.6 kg (SD = 24.7, $n = 335$). Elephant seal wean masses that were collected during this study (1993-1998) at Macquarie Island were similar ($p = 0.94$) to those collected between 1985 and 1991 (Burton *et al.* 1997), 118.8 kg (SD = 27.2, $n = 6504$) and 118.7kg (SD = 20.7, $n = 463$) respectively. However, the weaning masses at Marion Island were significantly different for these two periods ($p = 0.0001$) at 120.6kg (SD = 24.7, $n=335$) and 114.1kg (SD = 20.6, $n = 411$) respectively. Wean mass related to survival at both Islands (Fig4.5).

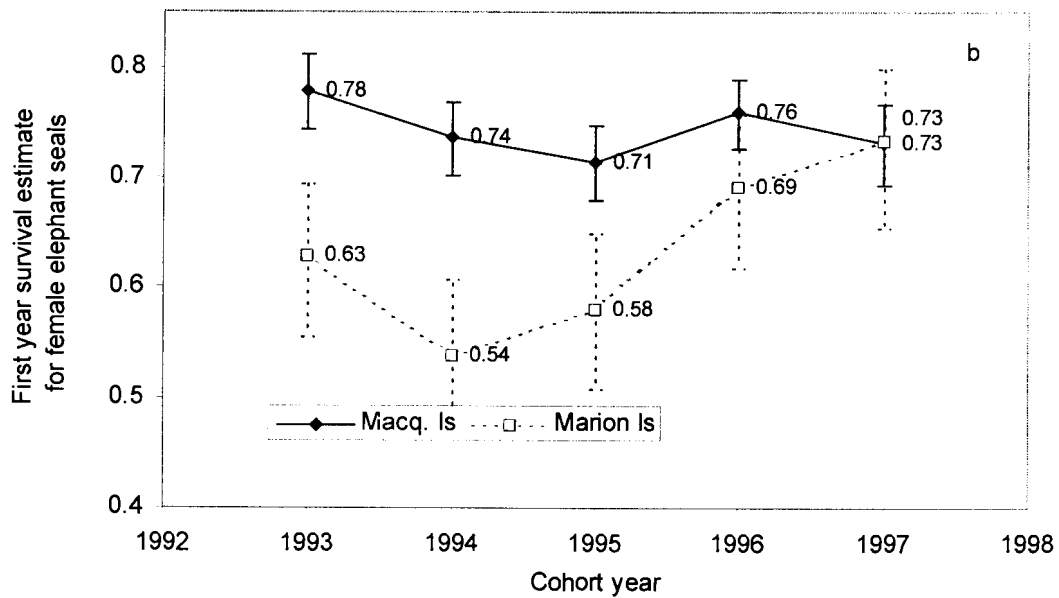
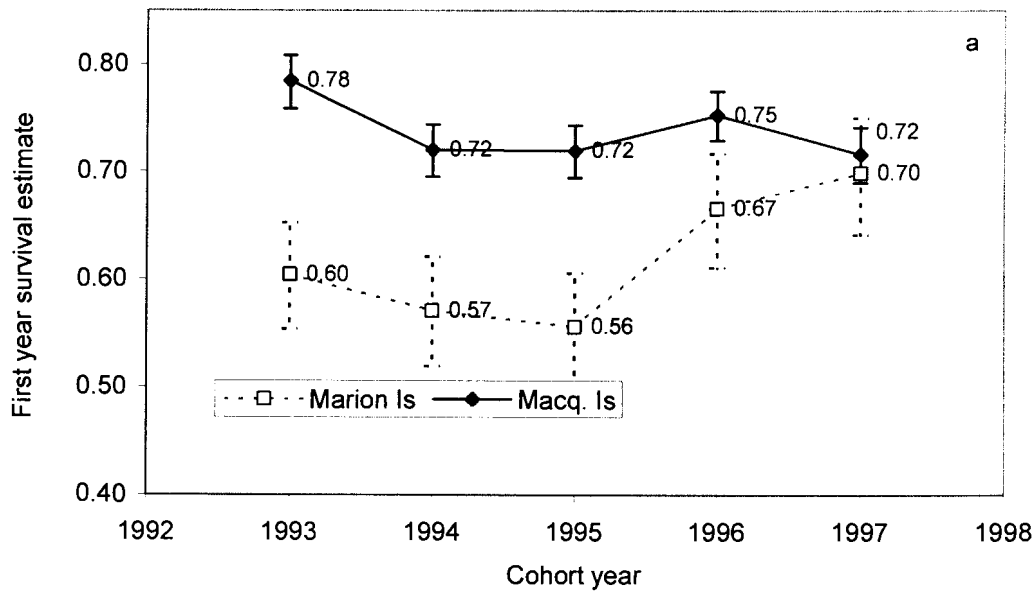
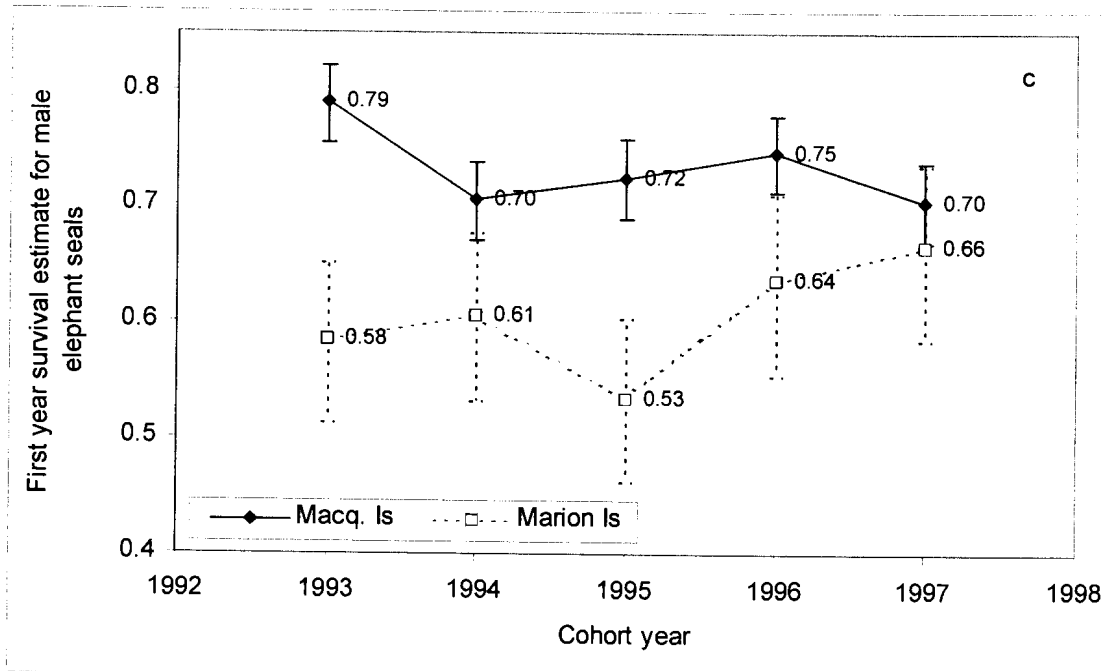


Figure 4.4. The concurrent first-year survival estimates (\pm 95 % confidence limits) for five cohorts Macquarie and Marion Island seals between 1992 and 1998, for: (a) male and female seals combined, (b) female seals and (c) male seals.

Figure 4.4 continued



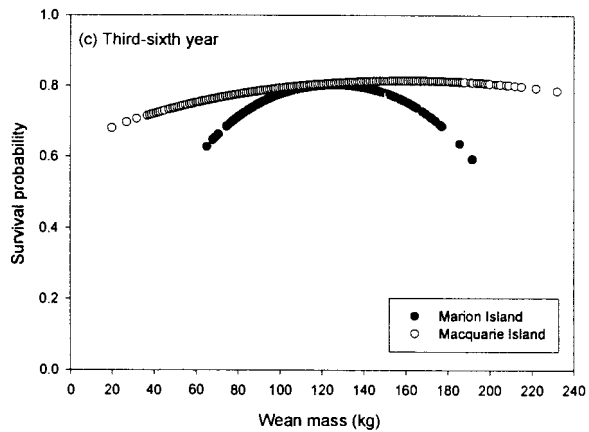
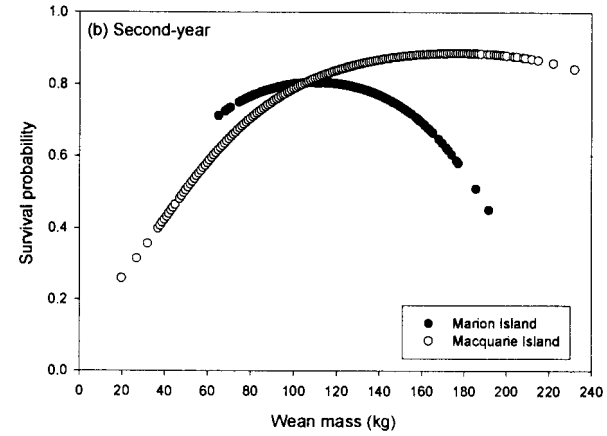
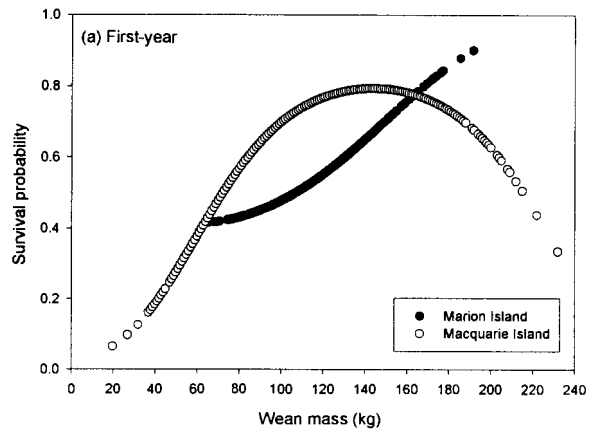


Figure 4.5. The relationship between elephant seal weaning mass and survival in the first two years of life and then for all ages over three years . Part a shows the non-linear relationship between wean mass and first-year survival, part b the non-linear relationship between wean mass and second-year survival and part c the lack of relationship between survival and wean mass after age three.

The most parsimonious survival models at each island location included wean mass as a covariate (Table 4.1). Wean mass influenced survival differently at the two island locations ($\chi^2_{16} = 38.66$, $p = 0.0012$) (Fig. 4.5). Wean mass influenced only first and second year survival at Macquarie Island but only first year survival at Marion Island (Table 4.1) and performed better than the model that included wean mass as a covariate for all age-specific survival estimates (ΔAIC 0.0 and 8.3). Moreover, at Macquarie Island first year survival was a polynomial function of wean mass and was most accurately described by the function; $y_{(survival)} = 2 \cdot 10^{-05}(\text{wean mass})^2 - 0.0012(\text{wean mass}) + 0.3799$ that accounted for more than 99% of the observed variation in first year survival ($r^2 = 0.997$). The relationship between wean mass and survival probability at Marion Island was best described by the exponential function $y_{(survival)} = 0.2369e^{0.0071(\text{wean mass})}$ which accounted for 99% of the observed variation in first year survival ($r^2 = 0.991$).

Mean age of primiparity and net reproductive ratio

The mean age at first breeding differed ($p < 0.001$) between the two island populations. At Macquarie Island, the mean age of first breeding was 4.68 years \pm 0.38, and at Marion Island, it was 3.95 years \pm 1.03. A significantly ($\chi^2_1 = 67.39$, $p < 0.0001$) greater proportion of three-year-old females breed at Marion Island (28.7%) than at Macquarie Island (1.2%) and the proportion of seals that have already bred at least once by age seven is greater at Marion Island than it is at Macquarie Island (Fig. 4.6).

The net reproductive ratio up to age 10 was lower at Marion Island than at Macquarie Island (Table 4.2 and Table 4.3), despite earlier initiation of breeding at Marion Island. Whilst these differences were greatest when it was assumed that all the females in a specific age class produced offspring (Table 4.3), the difference persisted even when the actual proportion of breeding females was used in the calculation of R_0 (Table 4.3).

Juvenile and early adult survival

The combined survival estimates for juvenile seals (1-3 years) differed between islands but survival of older seals (4-6 years) did not (Fig. 4.7). Overall there were significant differences in survival between the islands ($\chi^2_2 = 7.344$, $p = 0.0254$) with survival of elephant seals (ages 1-6 years) being greater at Macquarie Island than at Marion Island. Survival of older animals (4-7 years) was greater than juvenile survival at both islands (Fig. 4.7).

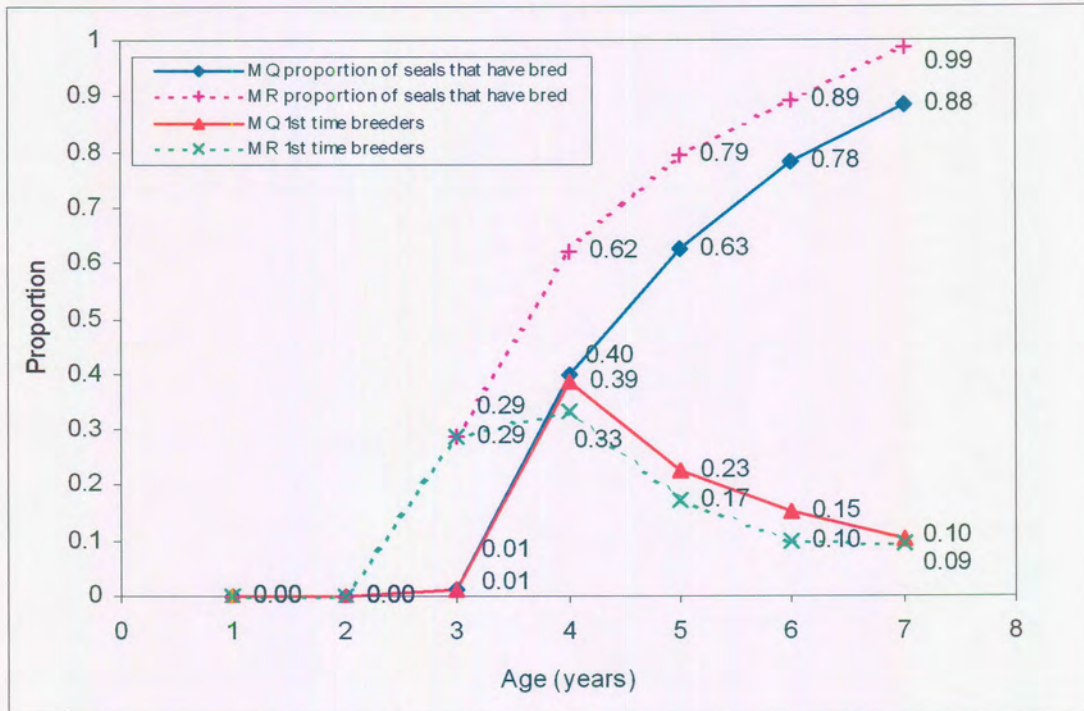


Figure 4.6. The total proportions of female seals breeding at Macquarie and Marion islands and the proportion of seals that breed for the first time in the first seven years of life.

Table 4.2. A life history table for female elephant seals to age 10 at Marion Island and at Macquarie Island. Included in the table are the survival probabilities p_x from age x to $x + 1$ values, the proportion l_x of individuals that have survived from birth to age x , and the mean number of female offspring m_x produced by a female seal while in a particular age class. The net reproductive rate R_0 to age 10 is presented for each population and defined as the $\sum l_x * m_x$. The annual rates of change for the two populations are -4.28% per annum and -1.48% per annum at Marion Island (Bradshaw personal communication) and at Macquarie Island (McMahon unpublished results) respectively.

Marion Island elephant seals					Macquarie Island elephant seals			
Age	p_x	l_x	m_x	$l_x * m_x$	p_x	l_x	m_x	$l_x * m_x$
0	0.628	1.000	0	0	0.7838	1.000	0	0
1	0.807	0.628	0	0	0.9121	0.784	0	0
2	0.783	0.507	0	0	0.7476	0.715	0	0
3	0.809	0.397	0.5	0.1985	0.8546	0.534	0	0
4	0.773	0.321	0.5	0.1605	0.8583	0.457	0	0
5	0.758	0.248	0.5	0.124	0.8106	0.392	0.5	0.1960
6	0.777	0.188	0.5	0.094	0.7761	0.318	0.5	0.1589
7	0.747	0.146	0.5	0.073	0.7554	0.247	0.5	0.1233
8	0.743	0.109	0.5	0.0545	0.8792	0.186	0.5	0.0931
9	0.753	0.081	0.5	0.0405	0.6417	0.164	0.5	0.0819
10	0.754	0.061	0.5	0.0305	0.6402	0.105	0.5	0.0526
$R_0 = \sum l_x * m_x = 0.577$					$R_0 = \sum l_x * m_x = 0.7058$			

Table 4.3. The adjusted net reproductive rate $R_{0 (adj)}$ to age 10 for female southern elephant at Marion Island and at Macquarie Island taking into account the actual proportion of seals known to have bred in each age group. $R_{0 (adj)}$ is defined as $\sum (l_x * m_x) b_x$ where b_x is the proportion of breeding females in each age group.

Age	Marion Island			Macquarie Island		
	$l_x * m_x$	b_x	$(l_x * m_x) b_x$	$l_x * m_x$	b_x	$(l_x * m_x) b_x$
0	0	0	0	0	0	0
1	0	0	0	0	0	0
2	0	0	0	0	0	0
3	0.1985	0.287234	0.057016	0.267209	0.011583	0.003095
4	0.1605	0.619455	0.099423	0.2284	0.400035	0.091353
5	0.124	0.79243	0.098261	0.1960	0.625846	0.122667
6	0.094	0.891152	0.083768	0.1589	0.779964	0.12392
7	0.073	0.986	0.071978	0.1233	0.882799	0.10886
8	0.0545	1	0.0545	0.0931	0.900	0.083832
9	0.0405	1	0.0405	0.0819	0.920	0.07534
10	0.0305	1	0.0305	0.0526	1	0.052551
$R_{0 (adj)} = \sum (l_x * m_x) b_x = 0.5359$			$R_{0 (adj)} = \sum (l_x * m_x) b_x = 0.6616$			

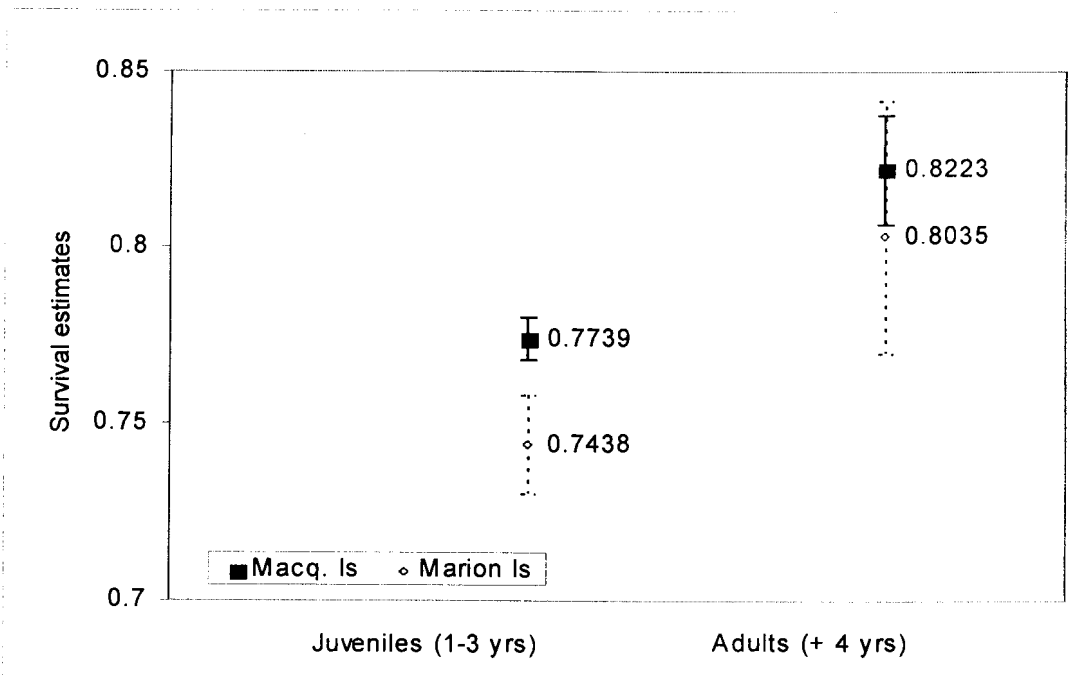


Figure 4.7. Concurrent juvenile and adult survival estimates ($\pm 95\%$ confidence limits) for juvenile (1-3 years) and adult (4-6 years) southern elephant seals at Macquarie Island and at Marion Island. Juvenile survival estimates were lower than adult survival estimates at both locations

Discussion

The recapture rates of marked southern elephant seals were higher at Marion Island than at Macquarie Island over the first seven years of life. These differences are likely to be a function of the much smaller pup production ($n = \sim 430$ pups) at Marion Island compared to Macquarie Island ($n = \sim 19\,000$ pups) so that resightings in harems and moulting aggregations were easier to obtain at Marion Island. Although concentrated in the Isthmus area, seals were dispersed around the entire 96 km coastline at Macquarie Island while at Marion Island the seals only occurred along the coast in the main study area (52 km), and were generally absent from the west coast.

Goodness of Fit

Non-compliance with the CJS assumptions, in particular the assumption that all animals have the same probability of survival, may have influenced survival rates but it is more likely to have affected the SE of these estimates (Carothers 1979). Although size, and therefore condition, at weaning influenced first year survival rates at Macquarie Island (McMahon *et al.* 2000), heterogeneity in capture probability is more likely to be the reason for the departures from homogenous survival probabilities (Pistorius, *et al.* 2002a). This is because juvenile seals are less philopatric than what adults are (Hofmeyr 2001). However, the CJS model is biologically sensible. This is because survival varies annually (Pistorius *et al.* 1999a), larger weaned seals have greater probabilities of survival (McMahon *et al.* 2000) and haulout behaviour and hence recapture probabilities vary with age (Hindell 1991; Hindell & Burton 1988b; McMahon *et al.* 1999) and season (see Pistorius *et al.* (2002a).

Juvenile survival

First year survival estimates for each of the five cohorts were more variable at Marion Island than at Macquarie Island and may indicate greater differences in female foraging success (prey distribution) and acquisition (prey availability) of resources (which influence maternal energy stores and transfer from mothers to their pups) for Marion Island females. This variability is related to maternal success because post-natal growth and survival are partly determined by the reserves a mother elephant seal has stored prior to breeding to provision her pup (Arnbom *et al.* 1997; Carlini *et al.* 1997; Fedak *et al.* 1996; Hindell & Slip 1997; McMahon *et al.* 2000). Female foraging success is an important component of population status because it affects juvenile survival (Hall *et al.* 2001; McMahon *et al.* 2000).

Wean Mass

Inter-island comparisons of wean mass provide a valuable tool for investigating the peculiar characteristics of the marine environment at each location (Burton *et al.* 1997). Wean mass remained unchanged during two periods of study at Macquarie Island suggesting that environmental conditions and/or the age distribution of foraging females have also remained constant. At Marion Island mean wean masses increased by approximately 5% over the same time, which suggests an increase in the quality, quantity, or both of prey or an increase in the ability of females to procure these prey. (Vergani *et al.* 2001) lend support to this view and demonstrated differences in elephant seal mean weaning mass believed to be a consequence of food availability subject to environmental perturbations caused by El Niño. Alternatively, the increase in wean mass at Marion Island may have occurred as a result of an increase in the mean age of females in the population, older females producing larger and heavier pups (Arnbom *et al.* 1993). The increase in wean mass at Marion Island could therefore be the outcome from an increase in the survival of older females rather than an increase in resources.

Primiparity

Marion Island females breed almost a year earlier than females at Macquarie Island. Because primiparity is related to body size and condition in seals (Laws 1956b) I hypothesize that female seals at Marion Island are achieving adulthood (in terms of breeding) at a younger age through faster growth rates. Elephant seals are “capital breeders”, i.e. animals that do not feed during the nursing period (Boyd 2000). Age at first breeding at Marion decreased from 4.4 years (Bester & Wilkinson 1994) to 3.6 years and at Macquarie Island it decreased from 5.2 years (Hindell 1991) to 4.68 years. This reduction in primiparity may indicate that seals at both locations are presently showing improved growth either because of increased resource availability in the seal’s Southern Ocean foraging grounds or a relative *per capita* increase in prey resources to the survivors. Furthermore, changes in reproductive parameters often occur after changes in population size that are caused by changes in food availability and climate change (Bowen *et al.* 1981; Lunn *et al.* 1994), as has been mooted for the Marion Island population (Pistorius *et al.* 2001). A reduction in age at first breeding may also be the consequence of individuals responding to selection pressure when densities are low (Stearns, 1983). However, this seems unlikely because in long-lived species like elephant seals there is a trade-off between current reproductive output and future reproductive success unlike small mammals that respond by investing wholly in current offspring (Stearns, 1983). Female elephant seals that breed before attaining a viable threshold size would

suffer greater mortality and so compromise their fitness, which seems contrary to the life history predictions for large long-lived mammals.

Greater resource acquisition can occur either through: (1) the resources being more available, (2) the females being more adept at acquiring these resources or (3) the resources being closer so that less energy is expended when the seals travel to and from foraging grounds. Evidence for clear differences in foraging behaviour of elephant seals of comparable ages and reproductive status in these populations is lacking although adult females of the two populations have thus far showed no overlap (Hindell *et al.* 1994b; Jonker & Bester 1998). There is however evidence of differences in productivity, and consequently resource availability, within the Southern Ocean (Smith *et al.* 1998; Smith *et al.* 1996; Wilson *et al.* 2001). Faster growth and earlier attainment of breeding size at the small Marion Island population compared to the large Macquarie Island population suggests greater *per capita* prey availability. The increased reproductive rate would consequently be responsible for increased population growth (Huber *et al.* 1991; Reiter & LeBoeuf 1991) and in the case of Marion Island, would have contributed to the possible stabilization of the population reported earlier (Pistorius *et al.* 2001). However, the stabilization of the Marion Island population over the period 1986 to 1997 (Pistorius *et al.* 2001) has been questioned (Bradshaw *et al.* 2002). Indeed the lower net reproductive ratios presented here (for the period 1993 to 2001) support the conclusions of Bradshaw *et al.* (2002). The overall rate (1976-1999) of population change (decrease) at Marion Island (-4.3%) is greater than that at Macquarie Island (-1.47%, AAD data, 1951-1999). Nevertheless, the differences in R_0 appear not to wholly justify the differences in population growth rates since the rates of population change appear to be disproportionately high in relation to the relatively small differences in R_0 . Similar observations have been demonstrated previously (Brommer 2000). Consequently, it appears that changes (increase in this instance) in fecundity have a limited influence on the rate of population change (Bester & Wilkinson 1994), and that the stabilization of the Marion Island population (Pistorius *et al.*, 2001) remains an open question.

Emigration and Predation pressure

Assuming that *per capita* prey abundance is more plentiful for the Marion Island population, the greater survival of juveniles (both sexes) and early-adults (females only) at Macquarie Island demands explanation. If the seals at Marion Island were growing faster and there were more resources available to them, their survival should be correspondingly higher unless there were more factors than resource limitation alone driving survival. Other factors such as predation

and/or disease (Hindell 1991; Hindell *et al.* 1994b) may be implicated. Very little permanent migration is possible granted the genetic differences (Slade *et al.*, 1998) of the populations at either Macquarie Island or Marion Island; and little emigration has been observed despite intensive beach searches at many sites (Bester 1988; Condy 1978; Guinet *et al.* 1992; Hindell & McMahon 2000; Nicholls 1970; Slade *et al.* 1998). Therefore, migration from these islands is not likely to contribute to differences in survival.

Killer whales (*Orcinus orca*, Linnaeus 1758) are predators of southern elephant seals (Condy *et al.* 1978; Guinet 1992b; Keith *et al.* 2001) and might play a significant localized role in the regulation of elephant seal populations (Condy *et al.* 1978; Guinet 1992b; Hindell 1991). When populations are large (such as at Macquarie Island), the effects of killer whale predation on elephant seal population dynamics may appear minimal. However, at lower populations the effects are probably more significant and may be sufficient to drive a population decrease (Trates *et al.* 1997). Similar numbers of killer whales occur at each island. At Macquarie Island there are approximately 20 different whales (Copson, 1994) and at Marion Island where there are between 25 and 30 individuals (Keith *et al.* 2001; Pistorius *et al.* 2002). At Macquarie Island the ratio of killer whales to seals is $2.9 \times 10^{-4}:1$ while at Marion Island it is $2.0 \times 10^{-2}:1$. Therefore, this considerable difference in predation pressure may in part account for the observed local differences in survival of juvenile elephant seals at Macquarie and Marion islands.

Causes for the differences in survival at Macquarie and Marion islands: a hypothesis

In summary, there are four important differences between the populations on Macquarie and Marion islands. The population at Macquarie Island (compared to that at Marion Island): (1) is larger (5.8 times), (2) has an age at first breeding that is almost a year later, (3) showed no changes in the mean annual wean-masses for the last seven years and (4) has less predation by killer whales. I interpret these differences to mean that:

(1) Intra-specific competition at Marion Island was greater than at Macquarie Island and that even though there was more food, competition for it would have been greater this is because the Marion island population is part of the greater Kerguelen stock which is much larger (~3 times larger) than the Macquarie stock (see Table 6.1). This is especially true in the first year of life when seals are naïve and for three-year-old female seals that are making the physical and physiological change from juveniles to adults when I observe the lowest rates of survival. Intra-specific competition would act in such a way that juvenile seals, that forage in different parts of

the water column to the adults (Hindell *et al.* 1991a; Hindell *et al.* 1999; Hindell *et al.* 1991b; Irvine *et al.* 2000; Slip 1997a; Slip 1997b) are unable to compete with older seals as they respectively: (1) enter a novel and foreign environment after weaning and (2) switch from juvenile foraging areas to adult foraging areas at the rapid onset of growth (Bell *et al.* 1997b; Bryden 1968b; Carrick *et al.* 1962a; McLaren 1993). This necessarily brings experienced foragers and inexperienced foragers into direct competition for limited and patchily distributed prey (McConnell *et al.* 1992; McConnell & Fedak 1996; McConnell *et al.* 1993). Indeed Slip (1997b) has suggested that there is considerable overlap between the foraging areas of adult and juvenile seals from Heard Island. Although this interpretation (Slip 1997b) lends some support to our argument, it needs to be treated cautiously because of the small sample sizes in the study. Younger seals do, however, develop and change their diving behaviour and by age two juvenile northern elephant seals (*Mirounga angustirostris*, Gill 1866) have developed diving abilities similar to those of adult seals (LeBoeuf 1994; LeBoeuf *et al.* 1996). It thus appears conceivable that relatively inexperienced seals older than two (in the third year of life) are competing with older more experienced seals for resources.

(2) That there has been an increase in the availability of resources within the Southern Ocean that allows females to grow faster and attain breeding size earlier. However, this increase has not been uniform around the Southern Ocean, there being a relatively greater availability of resources in the regions where the Marion Island seals feed (Wilkinson, 1992).

(3) That the increase in wean mass at Marion Island and the stability of the wean masses at Macquarie Island prior to 1992 and after 1993 is proof of (a) an increase in resources or (b) an increase in the mean age of females at Marion Island. The latter is unlikely because, for this to occur, juvenile survival rates would have to decrease relative to adult survival or adult survival would have to increase relative to juvenile survival over these two periods. Neither appears to have occurred at Marion Island (Pistorius *et al.*, 1999a, Pistorius *et al.*, 2001 & this study).

(4) That predation pressure is greater at Marion Island and so the mortality of juvenile seals there has increased. Thus, the lower overall rates of survival at Marion Island might be attributed to predation by killer whales.

Conclusions

Elephant seal population decreases in the southern Indian and Pacific Oceans appear to have been driven by resource limitations in the Southern Ocean. Sea-ice extent, one recognized determinant

of primary production in the Antarctic region of the Southern Ocean (Loeb *et al.* 1997; Nicol *et al.* 2000) decreased dramatically albeit not uniformly from the 1950s to the 1970s (de la Mare 1997) when southern elephant seal populations were decreasing most rapidly. This decrease in sea-ice has recently stabilized (de la Mare 1997) which suggests a corresponding stabilization in primary production as well. Such a stabilization of production at the lowest level of the food chain could be translated into stabilization of the entire food chain over time.

The decrease in primiparity at Macquarie Island and at Marion Island suggests that present population decreases in both populations may ameliorate, particularly at Marion Island where seals are breeding almost a year earlier than at Macquarie Island. As female seals are pupping earlier at Marion Island and Macquarie Island and because reproductive maturity is only achieved after seals have reached a minimum size (Laws, 1956), it follows that seals are likely to be growing faster if they reach breeding size earlier. I believe that more resources may be available to seals now than in the 1950's when elephant seal populations began decreasing. They perhaps can now achieve this minimum size earlier in life. Recent observations (de la Mare, 1997) of stabilization's in sea-ice around Antarctica appear to support our view of changes in food supply.

Regional differences in survival are partly the result of local differences in predator numbers for populations with greater predation pressure suffer greater mortality. It is likely that small populations are more prone to the negative effects of predators than larger populations (Guinet 1992a; Trites *et al.* 1997). Regional differences in productivity within the Southern Ocean may also dictate local differences in survival because of differences in prey availability as shown for Adélie penguins (*Pygoscelis adeliae*, Hombron and Jacquinet 1841) (Wilson *et al.* 2001). However, because elephant seals range and forage over widely in the Southern Ocean (Hindell *et al.* 1991a; Hindell & McMahon 2000; McConnell *et al.* 1992; McConnell & Fedak 1996) and because physical and environmental anomalies are transported around the Southern Ocean (White *et al.* 1998; White & Peterson 1996) it is difficult to relate seal life history variations to any localized physical or environmental anomaly. Therefore, resource variability would affect all seal populations such that it would be difficult to attribute small population differences in survival to global environmental variability. However, environmental variability can be expected to drive large-scale population changes (Barbraud & Weimerskirch 2001).

Elephant seal population decreases in the southern Indian Ocean and the southern Pacific Ocean were therefore probably driven by large-scale environmental change and ocean productivity in a similar manner to those shown for emperor penguins (*Aptenodytes forsteri*, Gray 1844) (Barbraud

& Weimerskirch 2001). Inter-island (population) differences are almost certainly the result of a complex interplay of predator pressure, intra-specific competition for resources and differences in resource availability in general. Intra-specific competition for resources is likely to be exacerbated in years when resources are limited and parameters such as survival can be expected to vary greatly at such times.

Chapter - 5 Modelling southern elephant seal populations: a comparison of populations with varying rates of change and observations of a population on a demographic knife-edge

Introduction

Identification of a population decrease operating over a decade or so may be the first indication that a species may be moving towards extinction. Management of decreasing populations requires more detailed information than simple population trends. One tool that is increasingly important, population viability analyses (PVA), which can help researchers and managers predict, with clear assumptions, the fates of declining populations (Reed *et al.* 2002). There are several models for PVA each with a suite of advantages and disadvantages (McCarthy *et al.* 2001b), but most rely on access to detailed life history data (Ellner *et al.* 2002). Such data are often difficult to obtain, particularly for large, long-lived animals. This makes assessment of population trajectories, and the development of hypotheses that address causal mechanisms, difficult. However, mathematical population models provide a means to test the relative contribution that each hypothesis makes at the population level (Caswell 2001; Cochran & Ellner 1992). Such models provide the link between the vital rates of survival and reproduction of individual animals and the population (Caswell 2001). Models can simulate the behaviour of the study population, and various variables within the model can be manipulated to test the effect of these changes at the population level (Caswell 2001).

A stage-structured matrix model is a useful facility to study the population dynamics of animal populations (Cochran & Ellner 1992). Such a case exists where age-specific survival and fecundity are dependent on body size. From such matrix models it is relatively straightforward to calculate the elasticities for each of the vital rates in the population matrix (Caswell 2001). ‘Elasticity’ is a measure of the relative sensitivity of a particular vital rate and can be defined as the effect on the population growth rate of a proportional change of a given fitness component (de Kroon *et al.* 2000). Analysis of these elasticities thus provide the ideal medium for the estimation of the proportional change in the population growth rate for a proportional change in the vital rates (Benton & Grant 1999; Caswell 2001; Grant & Benton 2000). Such elasticity analysis can be used: (1) to pinpoint the vital rates that contribute most to fitness and (2) to aid management decisions (Benton & Grant 1999).

Southern elephant seal (*Mirounga leonina*) populations at Marion Island and at Macquarie Island have continued to decrease (3.4% and 0.8% respectively) for at least the last 15 years (Bradshaw *et al.* 2002), while the Îles Kerguelen and Heard Island populations are believed (Guinet *et al.* 1999; Slip & Burton 1999) to have stabilised after a period of decrease. The South Georgia population has remained stable (Boyd *et al.* 1996) and the Peninsula Valdés has increased (Lewis *et al.* 1998). Although the reasons for these differences in population trends remain unknown, food (prey) availability is often hypothesized to be the ultimate factor determining population status (Hindell 1991; Hindell *et al.* 1994b; Pistorius *et al.* 1999b). It has also been suggested that predation from killer whales (*Orcinus orca*) may be a confounding factor especially in small populations (Guinet 1992a; McMahon *et al.* 2003; Trites *et al.* 1999). The mechanism whereby food availability impacts on population status remains contentious and two principal schools of thought exist: (1) that adult (particularly female) survival is important (Pistorius & Bester 2002a; Pistorius *et al.* 1999a; Pistorius *et al.* 1999b) and (2) that survival of juvenile seals and their recruitment into the breeding population are the principal driving forces (Hindell 1991; McMahon *et al.* 2003). Such contention is not uncommon and has also been reported from studies on large herbivores (e.g. cervids and bovids), illustrating the importance, and difficulty, in obtaining the necessary demographic data to make quantitative assessments of key demographic parameters, such as age specific mortality and fecundity (see Gaillard *et al.* (2000) for a review). Of course these explanations need not be exclusive and indeed both contribute to the determination of population size.

Using two concurrent long-term (16 years, 1986-2001) demographic data sets this study had two primary aims to: (1) simulate/project the population growth rates for three populations of southern elephant seals using life table information, (2) discover and describe the critical components in determining fitness (population growth rate) for each population, (3) assess the reliability of the model in predicting future population size and (4) generate hypothesis of life history agents driving population change.

Methods

Population trends

The southern elephant seals at Macquarie Island (Carrick *et al.* 1962b; Hindell & Burton 1988b), Signy Island (Laws 1956a) and Marion Island (Condy 1979) have a consistent and predictable annual haulout pattern. Indeed, the pattern of female haulout during the breeding period is so

predictable that it has been used as the basis for population estimates (Boyd *et al.* 1996; Galimberti & Boitani 2001; Hindell & Burton 1987; McCann & Rothery 1988). This is because it is more accurate to count adult females than it is to count pups and because the time they spend ashore can be quantified and hence maximum numbers can be determined quite accurately even when complete serial counts are not possible (Boyd *et al.* 1996; Galimberti & Sanvito 2001; Hindell & Burton 1988b; McCann & Rothery 1988). Population trends for the three island populations were calculated from previously published population counts from South Georgia Island (1951, 1985 & 1995) and Marion Island (1986 – 1997) (Pistorius *et al.* 1999b) and unpublished recent counts (1998 – 2001), while the counts for Macquarie Island were derived from a combination of previously published data and new counts (1949 - 2001) of female seals during the breeding season (01 September – 30 October) (Antarctic Division data). Daily counts were made from 1993 of all females present in the isthmus study area during the breeding season at Macquarie Island. The study area represents approximately 13% of all the females that breed on the island each year (Hindell & Burton 1987). The counts from the isthmus sub-population were used for three reasons: (1) they represent a long series of counts (38 counts between 1949-2001), (2) the counts are representative of, and mimic, the trends observed for the total island counts of breeding females (Hindell & Burton 1987) and (3) they provide a context within which to discuss the population trend seen during the 16-years covered by this study. The distribution of the daily counts throughout a breeding season fit a Gaussian curve (Hindell & Burton 1987). The following equation described the daily count data (i.e., number of females ashore) for each year's breeding season:

$$Y = ht \left(e^{\left(\frac{-0.5(x-\mu)^2}{SD} \right)} \right) \quad \text{Equation 1}$$

where: ht is the height of the curve (i.e., the maximum number of females ashore), μ is the day on which the maximum number of females was counted, and SD is the standard deviation of the number of days that seals were hauled out during the breeding season. The line of best fit for each year's breeding episode was determined using the least-squares technique described in Hindell & Burton (1987). This line provided estimates for the day of maximum number of seals present as well as the predicted maximum number of seals present on that day.

The rates of population change were expressed on the logarithmic scale because such rates are rarely constant linearly (Krebs 1999). The exponential rate of change (r) was then estimated as r

$= e^b - 1$ (Krebs 1999), where b is the slope of the fitted regression. These observed rates of population change were compared with the simulated rates of change derived from the projection of the age-specific fecundity and survival matrix.

Stochastic model

An age-specific-survival and age-specific-fecundity model was constructed. A separate life table was generated for each population. These data were collected from longitudinal capture-mark-recapture studies at Marion Island and at Macquarie Island and from a cross-sectional study from harvested seals at South Georgia. At Marion Island, seals ($n = 2\,000$) were tagged at birth with two plastic flipper tags and the subsequent resights, in the main study area (52 km of coastline), from 1993-2001 of five cohorts (1993-1997) formed the basis from which the life-tables were calculated. The practical details of this demographic study were previously summarized (Pistorius *et al.* 1999a; Pistorius *et al.* 2001). A contemporaneous group of seals were also marked and recaptured at Macquarie Island. At Macquarie Island, ~ 1000 seals/year were marked at birth with two plastic flipper tags when birth masses were measured. At weaning these seals were recaptured and their wean masses measured. Shortly after weaning (approximately three weeks) these seals ($n = 5\,000$) were permanently marked by hot-iron branding (McMahon *et al.* 1999; McMahon *et al.* 2000; McMahon *et al.* 1997). Daily searches of all the isthmus beaches (3.6 km), fortnightly searches of the northern third of the island (36 km), where most of the marked seals return to (Carrick *et al.* 1962b; McMahon *et al.* 1999), and monthly searches of all the islands beaches (96 km) were made to re-sight branded seals. Capture-history matrices were constructed from the resight histories of individual seals. Multiple resights within a year were treated as a single sighting. These capture matrices were used as input files for the capture-mark-recapture (CMR) program MARK (White & Burnham 1999) to estimate survival and capture probabilities from the resight records of the marked individuals. MARK provides survival (ϕ) and recapture (ρ) estimates under the Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965) and under several models that appear as special cases of the CJS-model (Lebreton *et al.* 1992). Reports of marked seals from sites other than Macquarie Island were rare (Hindell & McMahon 2000; McMahon *et al.* 1999; van den Hoff 2001).

The location-specific life-tables were converted into two-dimensional matrices that were used to project population change through time (Caswell 2001). The matrix has the form $L(n_t) X_{(t)} = X_{(t+1)}$, where L is the constant Leslie Matrix and $X_{(t)}$ is the age distribution of the population. The matrix L , and vector X are described below:

$$L = \begin{bmatrix} f1 & f2 & . & . & . & fn \\ s1 & & & & & \\ & s2 & & & & \\ & & . & & & \\ & & & . & & \\ & & & & s(n-1) & \end{bmatrix} \quad \text{Equation 2}$$

$$X_{(t)} = (X_{(1t)}, X_{(2t)}, \dots, X_{(nt)})^T$$

Where $f1$ is the fertility rate of females aged I and $s1$ is the survival probability of females at age i .

Concurrent known age-specific-survival-estimates and fecundity rates for Marion and Macquarie islands (McMahon *et al.* 2003) were used to describe the behaviour of the two island seal populations while historic cross-sectional data were used to describe the South Georgia population (McCann 1985). Although the data do not cover the maximal life-span of females (23 years) (Hindell & Little 1988), a near complete 20 year record is available for each island population. Survival and fecundity data for the seals up to age seven were used in the life tables and to complete the life tables the data were extrapolated to age 20 assuming constant female survival and fecundity (Pistorius *et al.* 2001). After 20 years approximately 0.1% of the original cohort members would have been alive (Pistorius & Bester 2002b).

I used a stochastic model which assumed that the variation in the vital rates is due to fluctuating environmental conditions (Fieberg & Ellner 2001). Environmental and intrinsic stochasticity was incorporated into the model by including a random iteration process as the measure of variation (Standard Deviation, SD, of the multiple cohort estimates of survival and fecundity) of the estimates observed between years. Survival (lx) and fecundity (mx) were adjusted at each iteration using a randomly selected value within the ranges described by the standard deviation. It was assumed that these data were normally distributed around the mean value. Because there were no estimates of the variance of estimates for the South Georgia Island life-history data (McCann 1985). I made this the mean of the variation observed at Marion and Macquarie islands. I used 1000 random iterations to calculate the mean projected population value using Monte-Carlo simulations (Caswell 2001). This procedure randomly selects a value within the given range of variability for each parameter (survival and fecundity) and recalculates the expected population number using this random variable. Each estimate was accompanied by an estimate of variance.

Elasticity of parameters

One of the advantages of using projection matrices to describe life-history data is that they facilitate data interpretation by directly linking the vital rates to population growth, i.e. λ (Caswell 2001). There are two ways of describing the proportional impact that age-specific survival and fecundity have on λ : (1) calculate the sensitivities of parameters and compare them, or (2) calculate the elasticities of the parameters and compare them (Caswell 2001). Because survival (which must vary between 0 and 1) and fecundity (which may vary between 0 and $mx > 1$) are measured on different scales it is preferable to use the dimensionless elasticity values of a particular parameter or group of parameters (Caswell 2001; Streams 1992) which is what was done. For elephant seals, survival varies between 0 – 1 but fecundity only varies between 0 – 0.5 (Benton & Grant 1999; Grant & Benton 2000) and thus it is appropriate to use the relative contribution rather than the absolute contributions. The age-specific elasticities were calculated for each island population to determine the influence of the age-specific vital rates on population growth, and secondly the elasticities were grouped into juvenile and adults to determine the phase-specific contribution to population growth. The elasticities (e_{ij}) thus quantify the proportional change in λ that results from a small change in the transition matrix a_{ij} . They were calculated from the general formula:

$$e_{ij} = \frac{\partial(\log \lambda)}{\partial(\log a_{ij})} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\lambda \partial a_{ij}} \quad \text{Equation 3}$$

At each island, juveniles were defined as those individuals in the non-reproductive ages, which varied between sites. The mean age at first reproduction was used as the delimiter between non-reproductive (juvenile) and reproductive (adult) individuals. The mean age at first breeding was 4.68 years \pm 0.38 and 3.95 years \pm 1.03 at Macquarie and Marion islands respectively (McMahon *et al.* 2003) and at South Georgia Island it was 4 years (McCann 1980). Thus at Macquarie Island, juveniles included females in all age classes up and including age five and adults were seals aged older than five. At Marion Island, juvenile females included seals up to age four, all seals older than four were adults, at South Georgia juvenile females were classed as such up to age four, and adult females were those seals older than that.

Validation of the modelled values

Stochastic models, such as the model used here, can be used to provide estimates of future population sizes. But because models are simplifications of much more complex systems it is important to validate the predicted values in some way. A standard deviates test (McCarthy & Broome 2000) was used here to determine the validity of the predicted values. Thus the predicted (modelled) values and the observed (annual counts) values can be compared by subtracting the observed population size from the mean predicted population and dividing by the standard deviation of the mean projected population size to generate a standard deviate for each of the years. If the model has predicted the mean population size accurately, the mean standard deviate would be zero. A single *t*-test of all years was used to test whether these mean values were different (McCarthy & Broome 2000).

PVA (Extinction times and the probability of extinction)

To estimate the probability of extinction a population viability analysis (PVA) was performed (Caughley 1994; Reed *et al.* 2002). Extinction was assumed to have occurred when the population fell below 20 individuals because the northern elephant seal population may have recovered to its present population levels from a remnant population of as few as twenty seals (Bonnell & Selander 1974). The PVA returns an estimate of the time to extinction of a population with given population parameters. The Monte-Carlo simulation program within POPTOOLS (Version 2.4.8, G. Hood, CSIRO, Australia) was used to calculate the extinction probabilities for the two populations at regular (10 year) intervals. I have assumed that the Macquarie Island population was closed because immigration has never been observed there and emigration is very limited (Nicholls 1970). However, there is some immigration at Marion Island (Bester 1988) and emigration from Marion Island has been recorded (Guinet *et al.* 1992). The effect of a small net positive rate of immigration to Marion Island from the larger populations in the Kerguelen Archipelago was tested and subsequently the breeding population at Marion Island was supplemented with one female seal in each age group (aged 1, 2, 3, and 4, i.e. 0.6, 0.8, 0.9 & 1.0% of the seals alive in each age class) annually and the simulations were re-run to quantify the effect of immigration on population persistence at Marion Island. To test the effect of greater immigrations rates the Marion Island population was supplemented further (eight seals) with an additional female annually in each of the four age classes above.

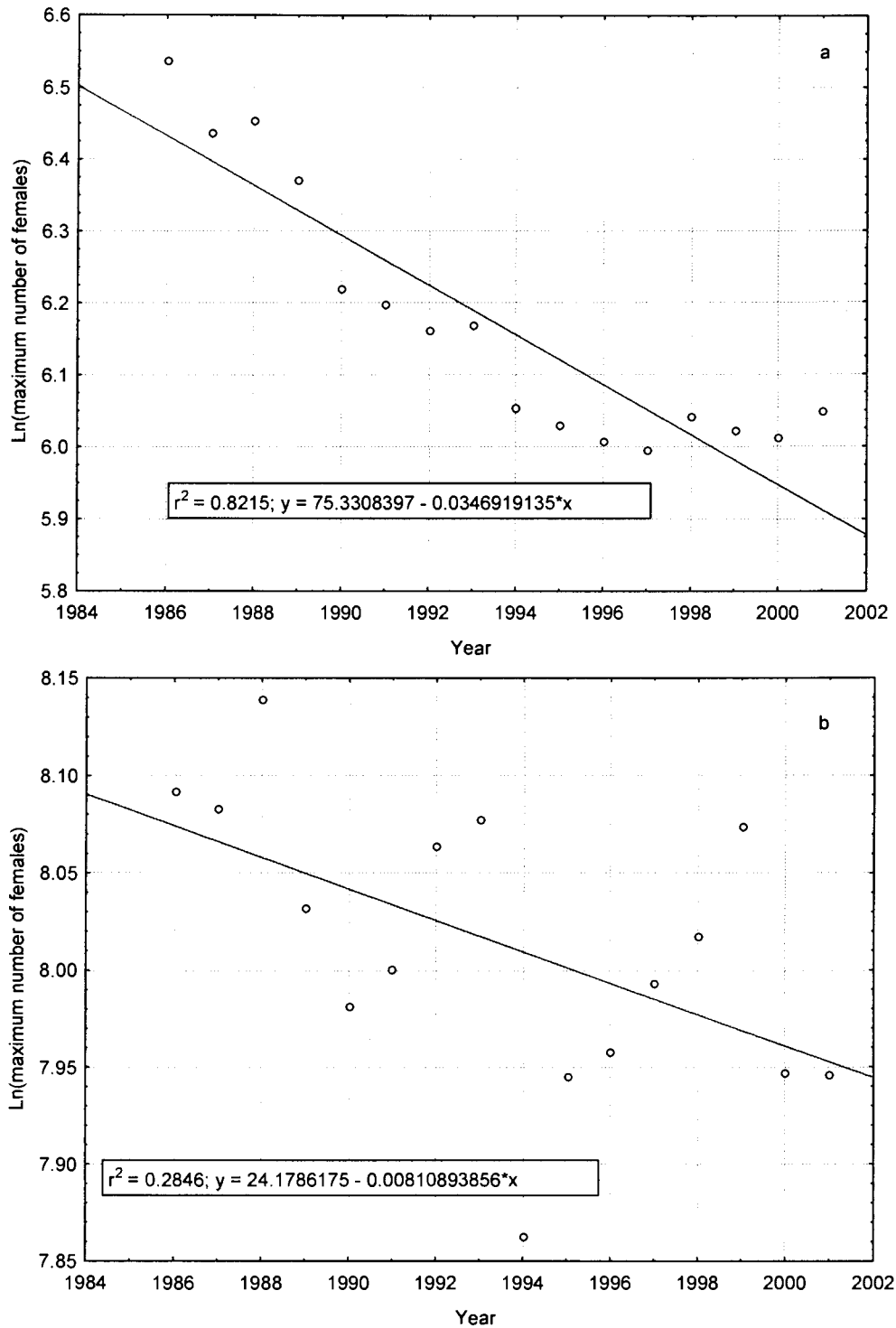
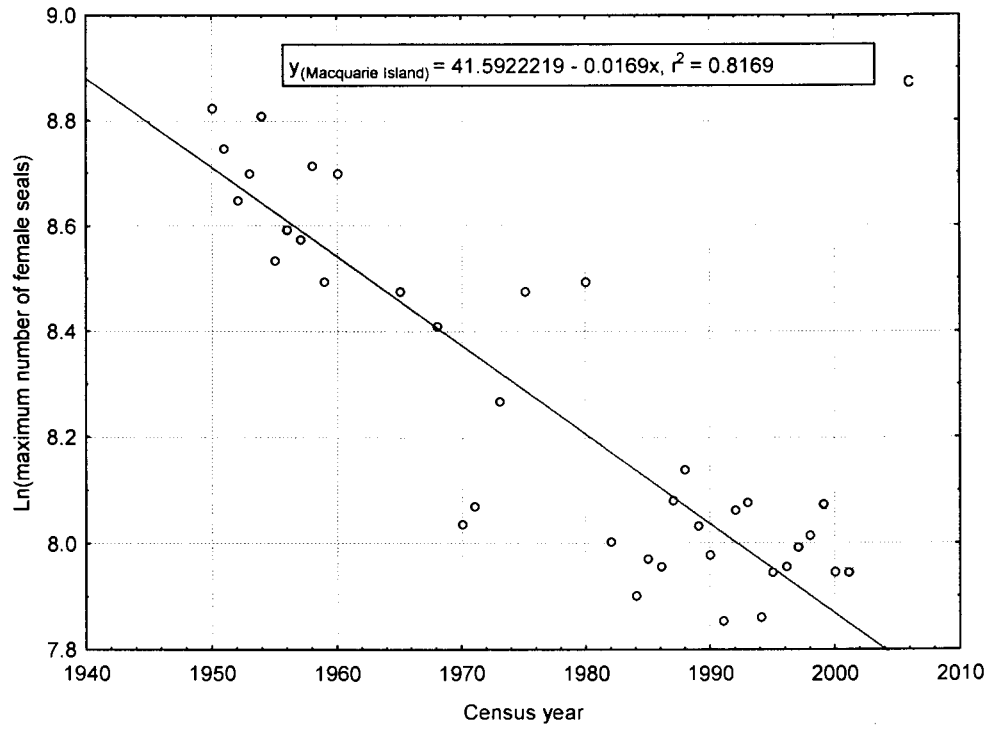


Figure 5.1. The elephant seal population decreases at Marion and Macquarie islands from 1986 - 2001 at (a) Marion Island and (b) Macquarie Island and (c) the long-term (1950 - 2001) decrease at Macquarie Island.

Figure 5.1 continued



Results

Annual census data

At both Macquarie Island and at Marion Island an annual count of all female seals ashore during the breeding season (1986-2001) was conducted to determine the maximum number of females ashore. For the 16 concurrent years that each of the elephant seal populations were monitored they decreased at overall constant rates of 3.41% and 0.81% at Marion Island and Macquarie Island respectively (Fig. 5.1a and 5.1b). In addition to the data for the concurrent 16-year data set a 51-year data set was also analysed for the Macquarie Island population. These analyses revealed that the longer-term (1950 – 2001) rate of change was -1.68% *per annum* (*pa*) (Fig. 5.1c) and that this rate had not changed in recent times (Fig. 5.2c). An analysis of the residual values was used to determine whether there had been any change in the rates of population decrease. There were no detectable changes in the rates of population decrease at Marion and Macquarie islands (Figs 5.2a, 5.2b & 5.2c).

There has been the suggestion of a recent stabilization of the Marion Island population (Pistorius *et al.* 2001) following analysis by a piece-wise non-linear function that described population change in two stages (1986 – 1994 & 1994 – 1997). Using this function, time (annual census) described 80% ($r^2 = 0.798$) of the variation in population size. However the fit was no better than a single stage function that described 80% ($r^2 = 0.797$) of the variation. Thus there is no statistically significant evidence to suggest a change in the rate of decrease at Marion Island from 1986-1997. Indeed when the same analyses are performed for the entire data set (1986 – 2001) there is again little difference between the piece-wise model ($r^2 = 0.828$) and the single stage function ($r^2 = 0.809$).

Because there was no evidence for any changes in the rates of population change at Marion Island and Macquarie Island, in either the short or long-term, the earliest known number of female seals counted was used as the initial population size and the number of female seals breeding annually was modelled. The first reliable counts of the maximum number of female seals were made in 1949 at Macquarie Island when 52 286 females were counted while the first reliable count at Marion Island was in 1976 when 1 173 females were estimated. Using the present life tables as input values for the Leslie matrix model, and using 1949 and 1976 as starting dates for each of the models, I predicted that there would be 474 female seals (95% CI 275, 780) at Marion Island and 28 792 (95% CI 13 153, 57 455) female seals at Macquarie Island in 2001. The actual

number of female seals counted at Marion Island in 2001 was 424 and at Macquarie Island it was 20 069. These counts were within the 95% confidence intervals around the mean estimate (Fig. 5.3).

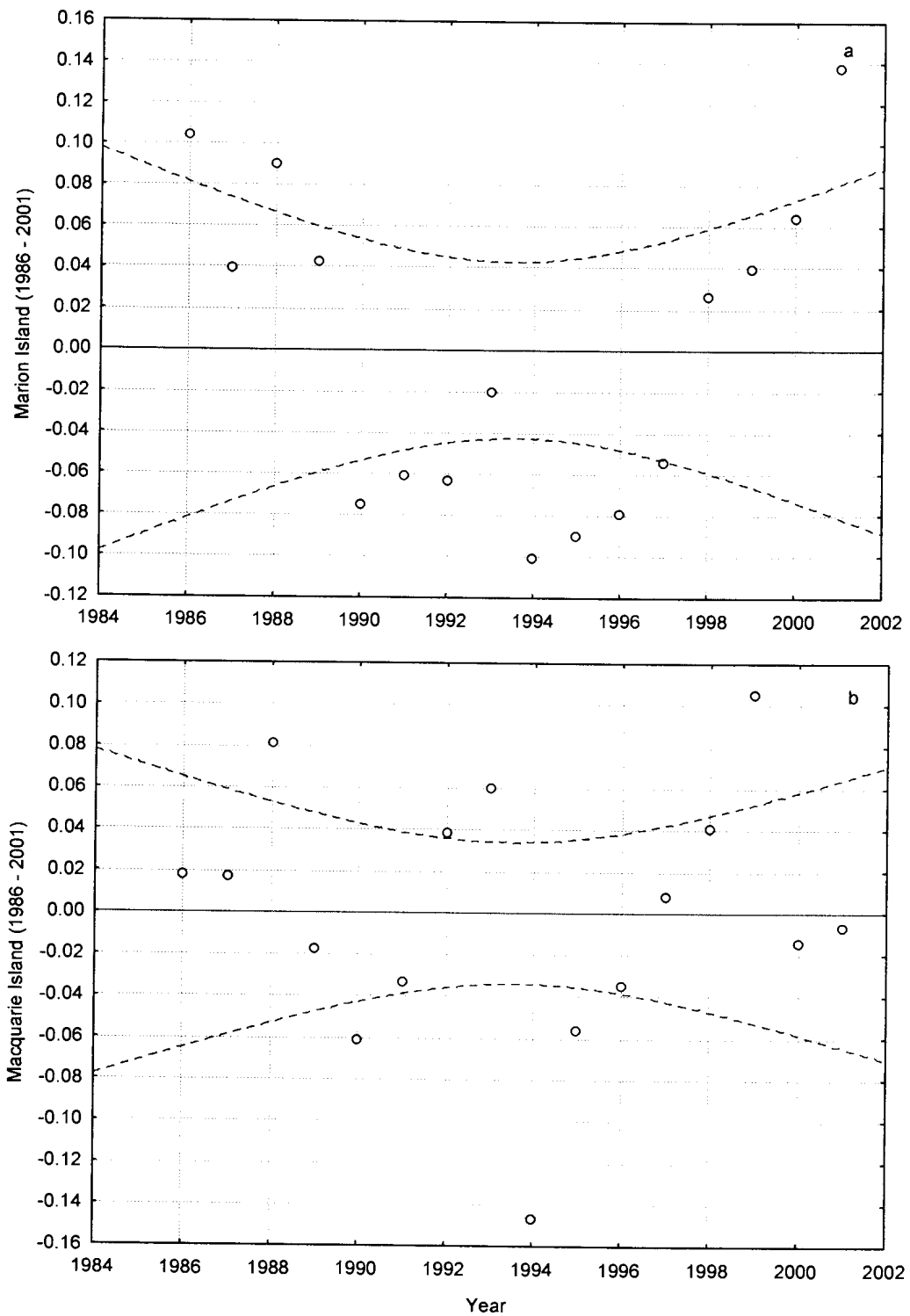
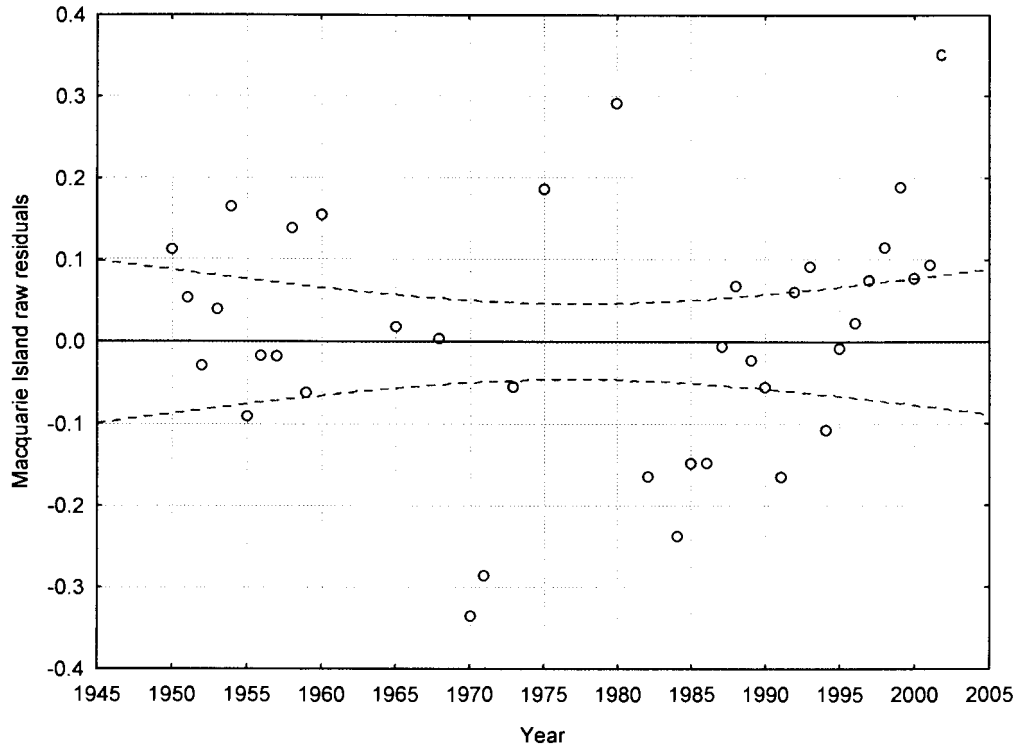


Figure 5.2. The results from the residual analysis of the annual rates of change from 1986 – 2001 at (a) Marion Island and (b) Macquarie Island and (c) the long-term (1950 – 2001) rate of change at Macquarie Island.

Figure 5.2 continued



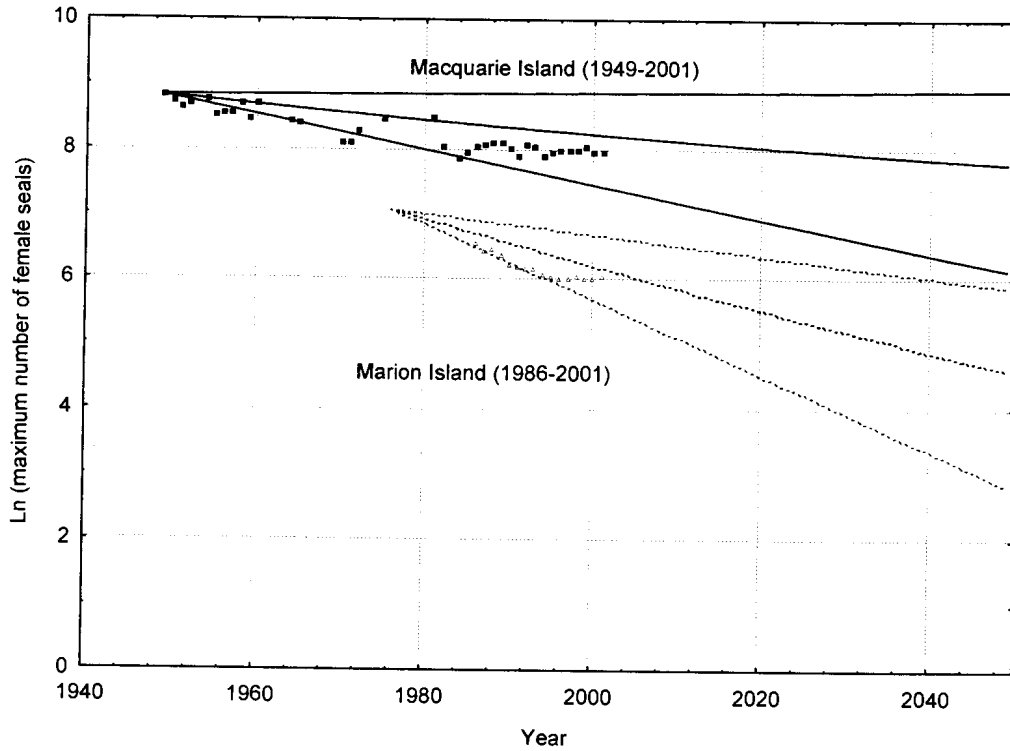


Figure 5.3. The empirical population counts of southern elephant seals at Marion Island (closed triangles) and Macquarie Island (closed squares) with respect to the predicted population numbers derived from the stochastic model and the upper and lower 95% confidence intervals.

Life tables and Leslie-Matrix models

Each mean estimate for survival (l_x) and fecundity (m_x) are presented (Table 5.1) along with the standard error ($\pm se$). These errors were used to calculate the upper and lower 95% confidence intervals for the estimates of survival and fecundity. The life tables (Table 5.1) and the extrapolations of these data showed that mean survival was higher at Macquarie Island than it was at Marion Island (Fig 5.4a & 5.4b). These differences were most pronounced in the first 10 years of life when survival was greater at Marion and Macquarie islands after which survival was greater at South Georgia. The survival curves for both islands were similar and showed a negative relationship between survival and age. At Macquarie Island, survival decreased at a constant ($r^2 = 0.997$) rate of 22.0% *pa*, while the mean annual rate of decrease was constant at Marion Island ($r^2 = 0.988$) at 22.5% *pa*. South Georgia Island was different to both Marion and Macquarie island in that the near constant ($r^2 = 0.842$) rate of decrease in survival was almost 3% greater (25.9% *pa*). There were no between-island differences in fecundity and all islands were remarkably similar, judging from the overlap in the 95% confidence intervals (Fig. 5.5). Seals breed at an earlier age at Marion Island than at Macquarie Island (Table 5.1) and there was an increase in fecundity with age. The maximum fecundity was reached after six years at Marion and South Georgia islands and after eight years at Macquarie Island.

Elasticities

Age-specific survival was an important parameter in the model of population growth for each of the three island populations (Table 5.2). The relative impact of age-specific survival on population growth at each island was more than 86% (88.4%, 87.0% and 87.5% at Macquarie, Marion and South Georgia islands respectively). Fecundity had a relatively small impact on population growth (12.5%, 14.3% and 12.0% at Macquarie, Marion and South Georgia islands respectively). While there were similar patterns in the relative sensitivities (elasticities) at each island that showed that juvenile survival had primary dominance on population growth, inter-island differences were also apparent. At Macquarie and South Georgia islands, juvenile survival had a greater effect (54% and 48% respectively) than adult survival (35% and 39% respectively) on population growth (r) than at Marion Island where juvenile and adult survival were equal (Fig.5.6). Fecundity did not play a major role in the growth of the populations, but it was interesting to note that the influence of juvenile and adult fecundities were similar at Marion Island but not at Macquarie and South Georgia islands. At Macquarie and South Georgia islands the influence of adult fecundity was greater than juvenile fecundity (Fig.5.6).

Table 5.1. Life tables for female elephant seals from Marion Island, Macquarie Island and South Georgia that were used to simulate the population growth rates at each island. The standard deviation (SD) of the estimates were used as a measure/proxy of environmental stochasticity.

Age	Marion Island				Macquarie Island				South Georgia Island			
	<i>lx</i>	SD	<i>mx</i>	SD	<i>lx</i>	SD	<i>mx</i>	SD	<i>lx</i>	SD	<i>mx</i>	SD
0	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
1	0.63	0.05	0.00	0.00	0.78	0.05	0.00	0.00	0.60	0.05	0.00	0.00
2	0.51	0.06	0.00	0.00	0.71	0.04	0.00	0.00	0.51	0.05	0.00	0.00
3	0.40	0.05	0.25	0.08	0.53	0.04	0.02	0.00	0.45	0.05	0.02	0.04
4	0.32	0.07	0.42	0.06	0.46	0.04	0.30	0.05	0.40	0.05	0.38	0.05
5	0.25	0.05	0.44	0.03	0.39	0.05	0.35	0.05	0.35	0.05	0.46	0.04
6	0.19	0.04	0.50	0.03	0.32	0.05	0.39	0.03	0.31	0.05	0.47	0.03
7	0.15	0.04	0.50	0.01	0.25	0.03	0.40	0.02	0.27	0.03	0.47	0.02
8	0.11	0.03	0.50	0.00	0.19	0.03	0.44	0.02	0.24	0.03	0.47	0.01
9	0.08	0.02	0.50	0.01	0.16	0.04	0.45	0.02	0.21	0.03	0.47	0.01
10	0.06	0.02	0.50	0.02	0.11	0.02	0.47	0.02	0.18	0.02	0.47	0.02
11	0.05	0.02	0.50	0.01	0.08	0.02	0.47	0.02	0.16	0.02	0.47	0.02
12	0.05	0.02	0.50	0.01	0.07	0.02	0.47	0.02	0.14	0.02	0.47	0.02
13	0.04	0.01	0.50	0.04	0.06	0.01	0.47	0.02	0.11	0.01	0.47	0.03
14	0.03	0.01	0.50	0.01	0.05	0.01	0.47	0.02	0.08	0.01	0.47	0.02
15	0.03	0.01	0.50	0.02	0.04	0.01	0.47	0.02	0.06	0.01	0.47	0.02
16	0.02	0.01	0.50	0.00	0.03	0.01	0.47	0.02	0.04	0.01	0.47	0.01
17	0.02	0.01	0.50	0.02	0.03	0.01	0.47	0.02	0.02	0.01	0.47	0.02
18	0.01	0.01	0.50	0.02	0.02	0.00	0.47	0.02	0.01	0.01	0.47	0.02
19	0.01	0.01	0.50	0.02	0.02	0.00	0.47	0.02	0.00	0.01	0.47	0.02
20	0.01	0.01	0.50	0.01	0.01	0.00	0.47	0.02	0.00	0.00	0.47	0.02

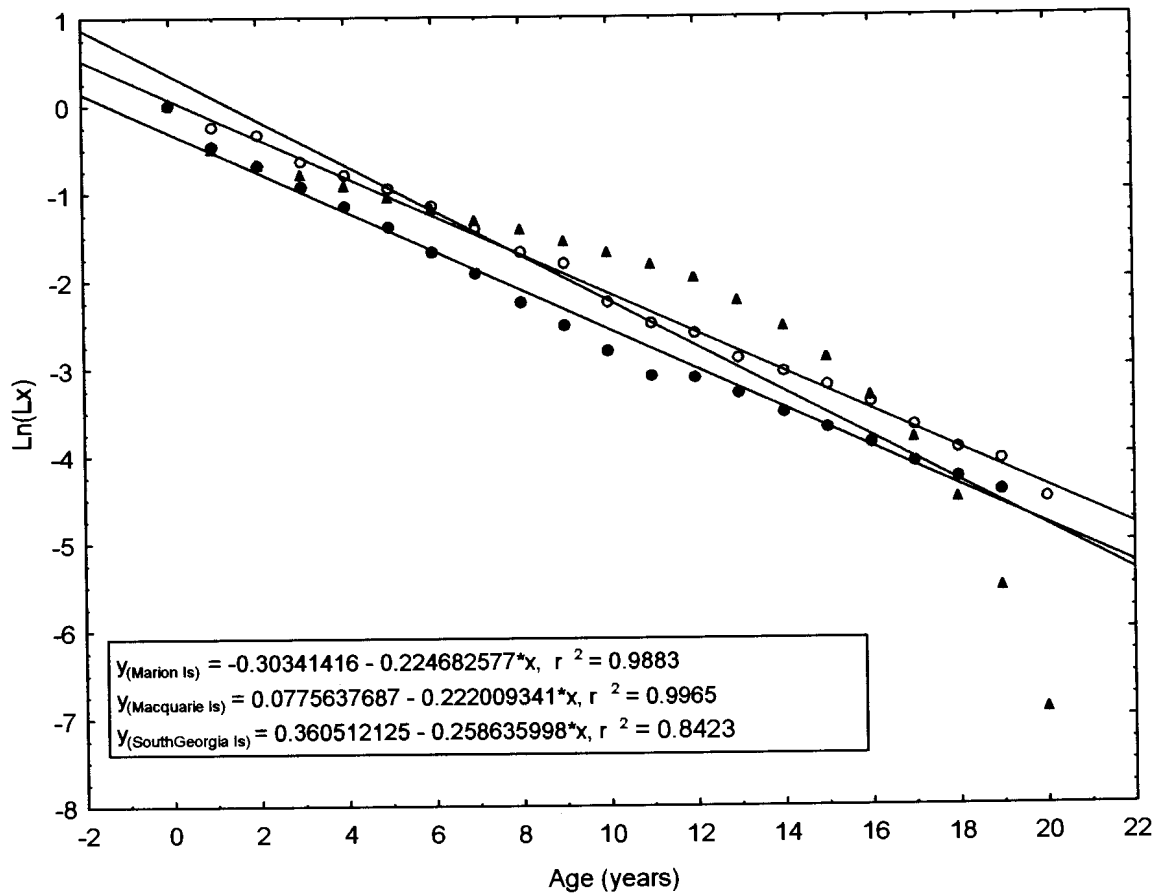


Figure 5.4. The mean log transformed survivorship curves for three elephant seal populations at Marion (closed circles), Macquarie (open circles) and South Georgia (closed triangles) islands.



Figure 5.5. The mean fecundity curves with the 95% confidence intervals for the three elephant seal populations at Marion (closed circles), Macquarie (open circles) and South Georgia (closed triangles) islands respectively.

Table 5.2. The age-specific elasticities for each of the island populations studied: (a) Marion Island, (b) Macquarie Island and (c) South Georgia Island.

Age	Marion Island		Macquarie Island		South Georgia Island	
	lx	mx	lx	mx	lx	mx
0	0.000	0.000	0.000	0.000	0.000	0.000
1	0.116	0.000	0.130	0.000	0.125	0.000
2	0.116	0.000	0.130	0.017	0.125	0.000
3	0.115	0.001	0.113	0.030	0.127	-0.001
4	0.103	0.019	0.088	0.022	0.107	0.013
5	0.089	0.021	0.069	0.012	0.088	0.016
6	0.077	0.014	0.058	0.015	0.073	0.016
7	0.063	0.014	0.052	0.007	0.059	0.014
8	0.050	0.012	0.045	0.007	0.044	0.011
9	0.038	0.012	0.038	0.008	0.035	0.009
10	0.029	0.005	0.032	0.005	0.028	0.010
11	0.023	0.004	0.030	0.005	0.022	0.008
12	0.018	0.005	0.025	0.003	0.015	0.007
13	0.014	0.003	0.018	0.003	0.011	0.005
14	0.012	0.003	0.013	0.001	0.007	0.004
15	0.009	0.002	0.010	0.002	0.004	0.003
16	0.006	0.003	0.009	0.002	0.003	0.002
17	0.004	0.002	0.007	0.001	0.001	0.001
18	0.002	0.002	0.003	0.002	0.001	0.0002
19	0.001	0.001	0.002	0.0000	0.0003	0.0004
20	0.0000	0.001	0.0000	0.0000	0.0000	0.0001

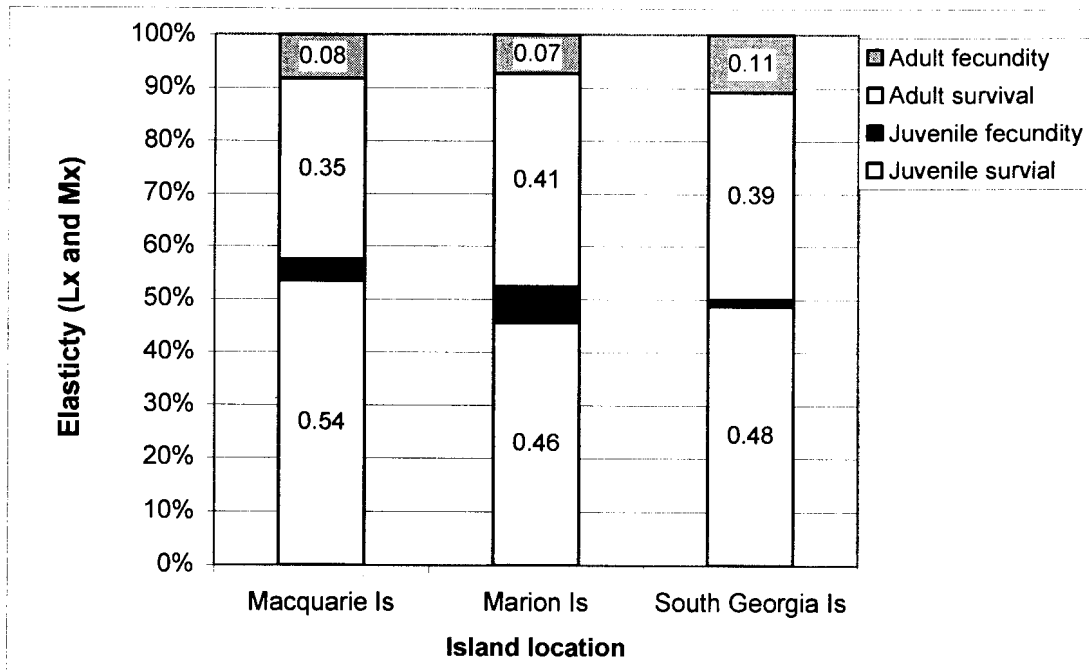


Figure 5.6. The relative sensitivities (elasticities) of the vital life-history traits: juvenile survival, juvenile fecundity, adult survival and adult fecundity on population growth/fitness.

Population trajectories

The stochastic Leslie-matrices formed the basis from which I projected/modelled the population growth of each island population. By incorporating some form of environmental variability into the model, in the form of the variation around the mean estimates of survival and fecundity, I was able to not only project the mean population trends but to also project upper and lower confidence intervals for the estimated trend (Figs 5.7a, 5.7b & 5.7c). These projections suggested that: (1) it seems unlikely that the South Georgia population will change appreciably within the next proposed census period of 10 years, (2) that the Marion Island population will continue to decrease given the present survival and fecundity estimates and (3) that the Macquarie Island population seems close to stability. The matrix projections for Macquarie Island show that the population may continue to decrease at near the present rate but it may stabilize or even increase given very small (*circa* 5%, i.e. the upper estimates of variance) changes in survival and fecundity rates. The modelled probability that the finite rate of increase at Macquarie Island is greater than 1 was found to be 0.034 after 5000 iterations. This means that there is a 1 in 29 chance of the population increasing if everything remains the same.

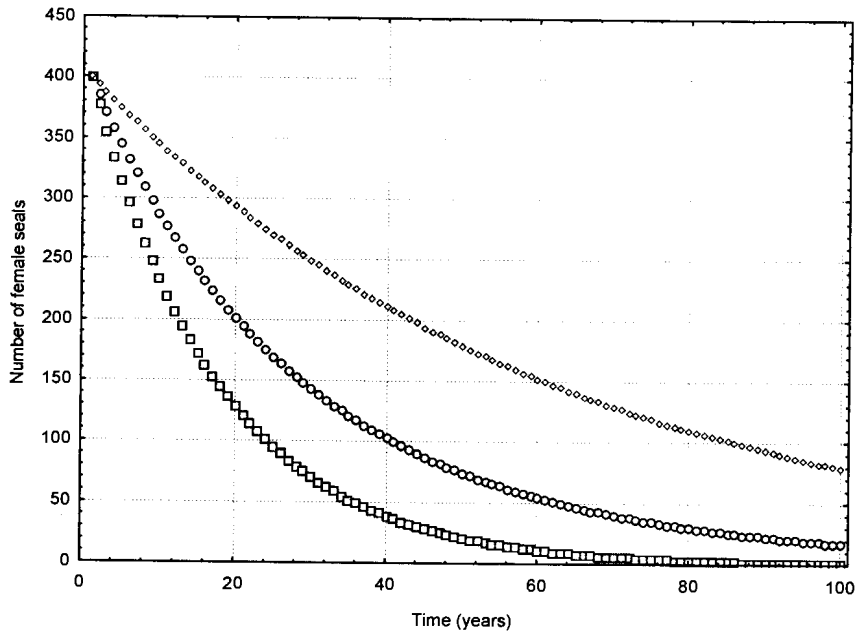
Validation of the predicted values

The stochastic model used here is consistent with the measured seal population sizes from 1986 to 2001 (Table 5.3) at Marion Island ($t_{15} = 0.130$, $p = 0.260$) and at Macquarie Island ($t_{13} = -0.408$, $p = 0.690$). But, when applied to longer periods of prediction such as from 1976-2001 at Marion Island and from 1949-2001 at Macquarie Island, the model was unable to predict the population sizes ($t_{16} = -1.587$, $p = 0.06$ & $t_{26} = -7.838$, $p = 2.6 \cdot 10^{-8}$ respectively) that were censused.

PVA Extinction times and the probability of extinction

Calculation of the time to extinction for the two decreasing populations at Macquarie and Marion islands (if all demographic parameters remain unchanged) showed that there was an imminent risk of extinction (*circa* 100 years) for the Marion Island population but not for the Macquarie Island population (Fig. 5.8). The mean time to extinction for the Marion Island population was 134 years (105-332 years). At Macquarie Island the mean time to extinction was 564 years and an earliest time to extinction of 307 (lower 95% confidence limit) years. The upper 95% confidence limit could not be calculated because the population increased. The probability of extinction after 100 and 150 years was 0.71 and 1.00 respectively for Marion Island and 0.000 and 0.000

respectively for Macquarie Island. When immigration was introduced into the model at Marion Island (Bester 1988) these probabilities of extinction decreased. The probability of extinction after 100 and 150 years was 0.355 (SE 0.010) and 0.567 (SE 0.016) respectively when the population was supplemented annually with four females, one of each age, aged one, two, three and four. When the population was supplemented by a further eight females, two in each of the proceeding ages, these probabilities decreased further to 0.000 (SE 0.000) and 0.003 (SE 0.0012) respectively.



a

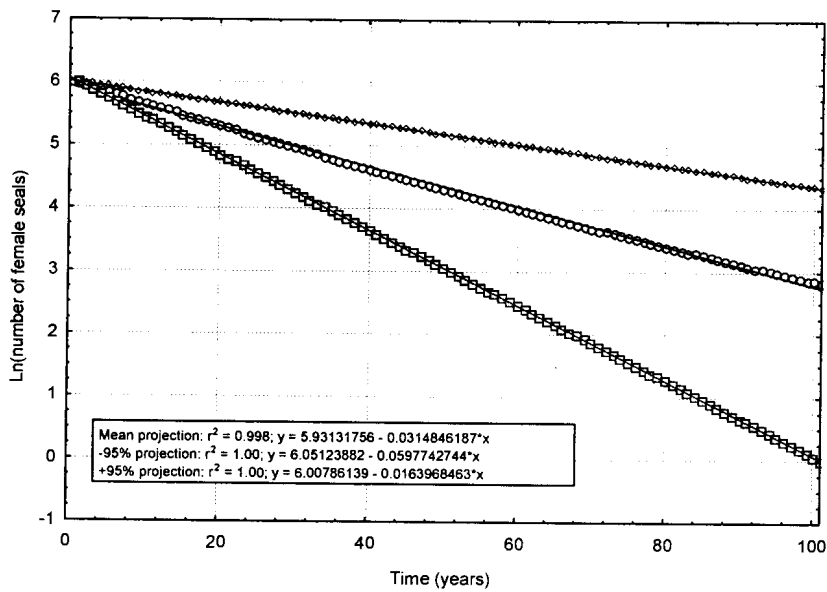
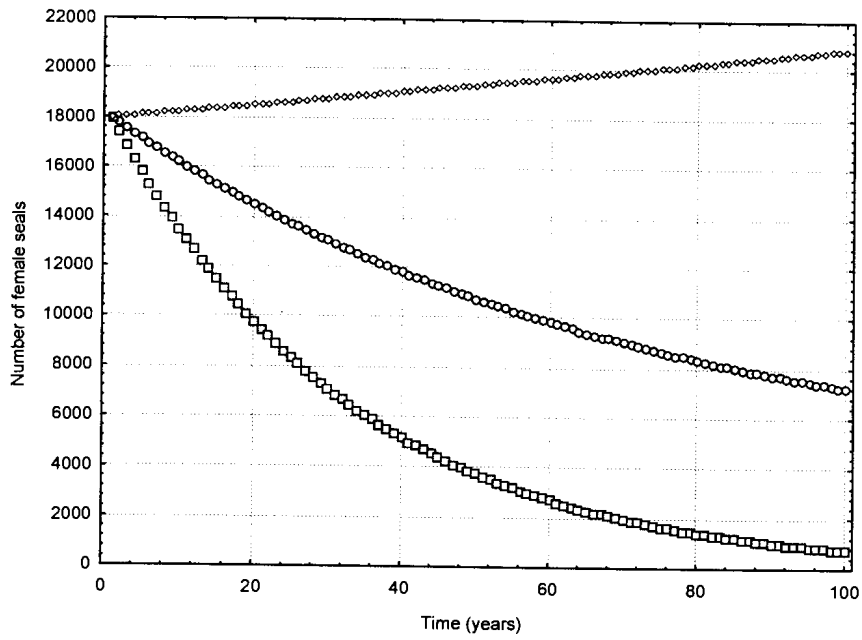


Figure 5.7. The projected population trajectories of the three island populations studied: (a) Marion Island, (b) Macquarie Island and (c) South Georgia Island. These trajectories were calculated and projected from a matrix-model that randomly selected survival and fecundity values within a defined range (SE) around a mean.

Figure 5.7 continued



b

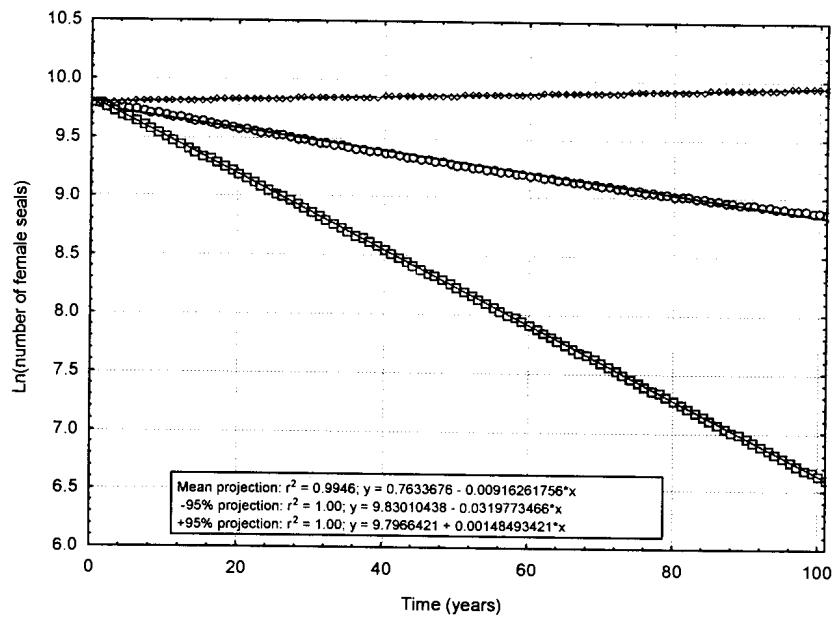
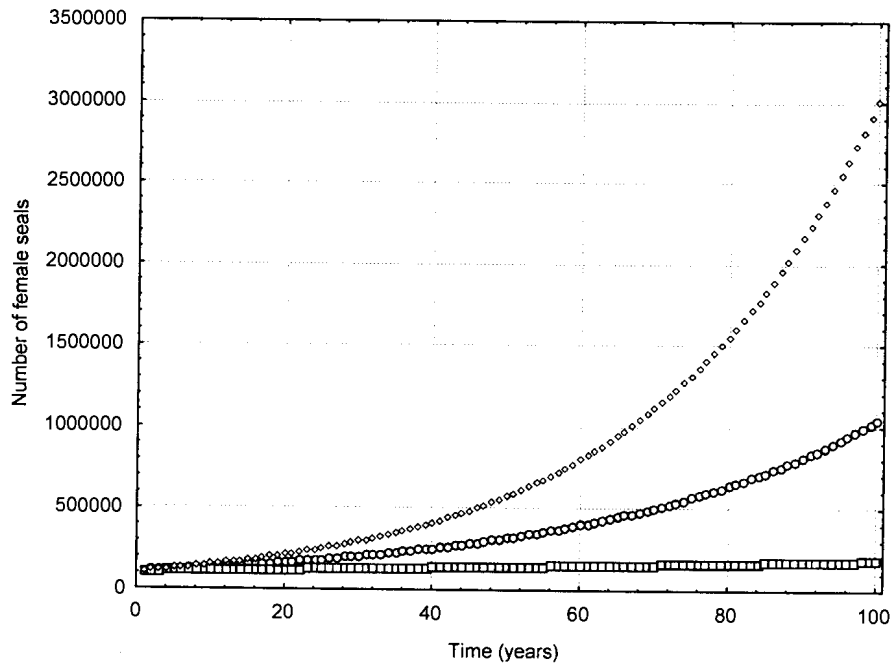


Figure 5.7 continued



c

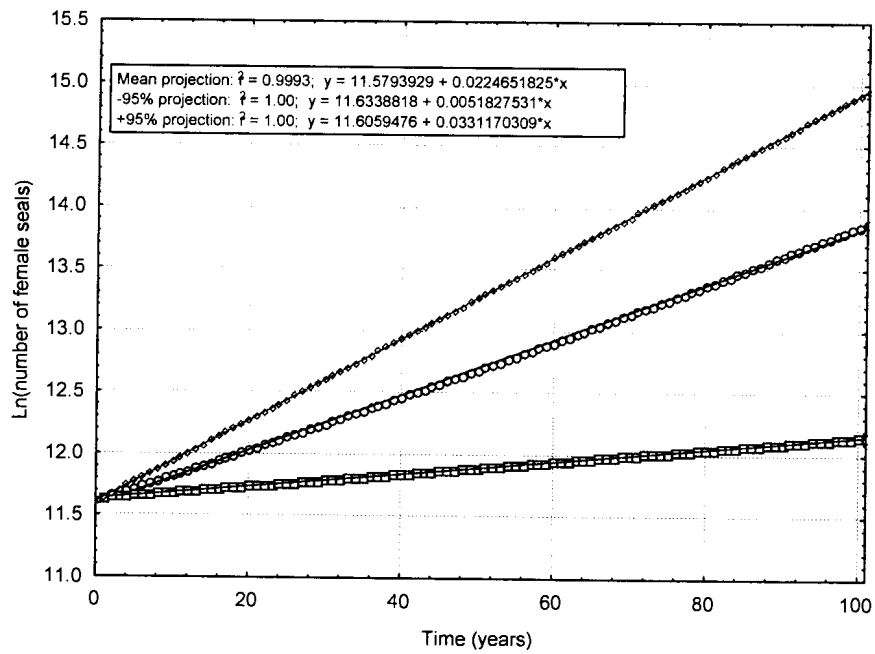


Table 5.3. The mean predicted and empirical life-history rates for Marion, Macquarie and South Georgia islands.

		Modelled result	Empirical result
Overall rate of change (per annum)	Marion Island (1986-2001)	-3.20%	-3.41%
	Macquarie Island (1949-2001)	-1.55%	-1.69%
	South Georgia Island	0.25%	0.19%
Number of female seals in 2001	Marion Island	477 (\pm 68)	424
	Macquarie Island	28 792 (\pm 10740)	20 069
	South Georgia Island	128 172 (\pm 1 677)	Unknown
Generation times (years)	Marion Island	7.60	
	Macquarie Island	7.90	
	South Georgia Island	8.23	

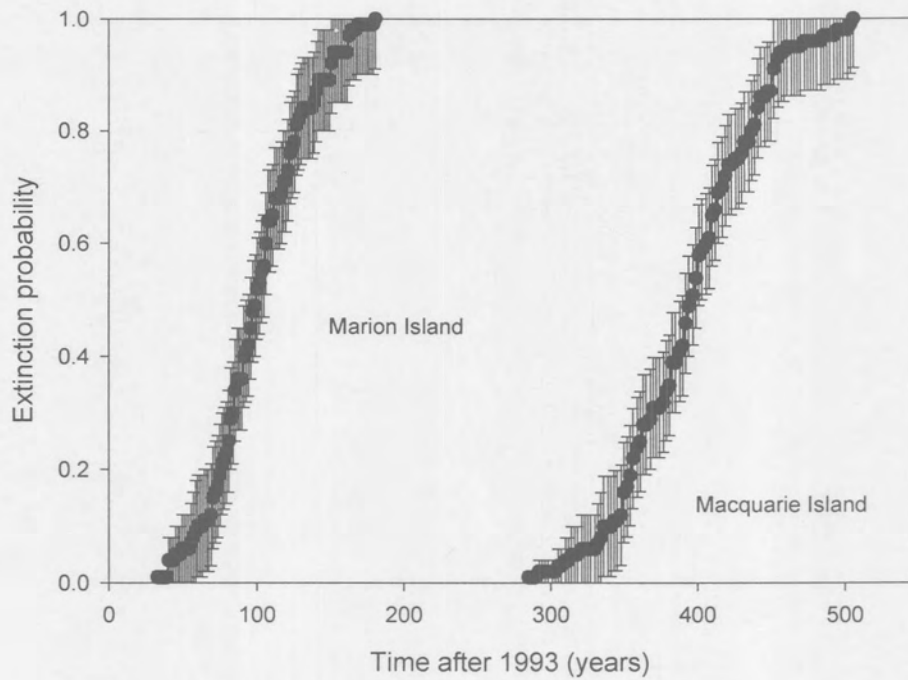


Figure 5.8. The extinction probabilities for two declining populations of southern elephant seals at Marion Island and Macquarie Island.

Discussion

This study represents one of the few long-term and longitudinal studies of pinniped demographics. It was initiated to identify the reasons and mechanisms for the overall decreases in elephant seal populations observed in the Indian and Pacific oceans. The magnitude of these decreases in the elephant seal populations at Marion Island and at Macquarie Island have been 63.9% and 58.5% in the past 25 and 51 years respectively. The reasons for these decreases are still unknown but now much more is known of southern elephant seal ecology (McMahon *et al.* 1999; McMahon *et al.* 2000; Pistorius *et al.* 1999a; Pistorius *et al.* 1999b). The modelling component of the study was used to generate hypotheses about how sensitive the populations were to changes in a number of possible demographic parameters. An important finding here was that population change seemed to be very sensitive to changes in juvenile survival, although evidence to the contrary has been presented (Pistorius & Bester 2002a). Determining the factors (e.g. foraging behaviour and predation) that most affect juvenile survival may therefore assist in understanding population change. The strength of the present study is the fact that there were concurrent data for two populations from two different stocks with these data collected in similar ways and with consistent search effort. Longitudinal studies such as this one are rare because they require large investments of time to mark and recapture long-lived large mammals as southern elephant seals that have a maximum recorded life span of 23 years) (Hindell & Little 1988).

In addition to the longitudinal life-history data that were available for this study, and from which a stochastic model could be constructed, there were also total populations counts made concurrently at each location with which the predictions from the model could be compared. Indeed, despite models being commonly used to predict population trends and viability, many are not validated with field data because such data are uncommon (Brook *et al.* 1997). The Leslie-Matrix model estimated population trends for the two populations in which there were no differences from the observed rates of change for each island population. The models provided estimates for the rates of change of the populations and also provided predictions (with confidence limits) for the numbers of adult female seals alive in 2001. This prediction, using the 1986-2001 data, encompassed the number of adult female seals actually alive in the short-term. But the model, using the 1949-2000 data, was unable to predict with any accuracy the number of seals in 2001. Predictive models are not often used for long-term predictions beyond a period approximately 20% of the length of the data/time-series (Reed *et al.* 2002).

While there have been suggestions that these (Marion Island and Macquarie Island) populations may have recently stabilized (Hindell *et al.* 1994b; Pistorius *et al.* 2001), other studies using published census data from the Marion Island population 1986-1997 (Bradshaw *et al.* 2002) and this study do not support this. These conclusions do not preclude the possibility of a change, but I propose that the time series has not been long enough to detect statistically significant changes.

Thus no changes in the rates of decrease were detected at either Marion Island or Macquarie Island over the duration of this study (1986-2001). The rates of decrease detected in this study are lower than those estimated in previous studies (Bradshaw *et al.* 2002; Hindell *et al.* 1994b). This is because the 16-year data set (which is a subset of a much larger 51-year data set) for Macquarie Island showed that the population had decreased at a constant rate of 1.68% per annum during the past 51 years, which is an average of 51 years of quite variable data. During this time there were many fluctuations with short periods of apparent increase and periods of quite pronounced decrease (this study). The 16-year subset may represent a phase of decreased rate of change, within the overall data set; but until a longer time series becomes available it cannot be determined whether this is a more recent trend of the population. However, it was during this period of relatively slow decrease that the demographic data used in the models were collected.

Interpretations of these rates of change need to be treated cautiously because small sets of data, or subsets of data may incorporate short-term changes in environment or recruitment and may not be truly representative of actual population trends as has been shown previously (Bradshaw *et al.* 2002) and shown here.

Key demographic parameters influencing the rates of change

Juvenile survival was identified as the most sensitive factor determining population growth at all three islands. Consequently, the models suggest that the population growth rates of elephant seals were much more sensitive to variations in juvenile survival than the same degree of variation in any of the other fitness components. In contrast Pistorius *et al.* (2002) found no differences in the probability of survival of juveniles (1-3 years) at Marion Island during the period. They defined 1983-1994 as a period of decrease and 1994-1999 as a period of stabilization. They then dismissed juvenile survival as an important population-regulating component for southern elephant seals at Marion Island. This interpretation is contentious because it depends on the premise that there had been a change in the status of Marion Island population (Pistorius & Bester 2002a).

Juvenile survival may be seen to be the composite of first, second and third year survival as few (<5%) of these age-class females were recruited to the adult/breeding population. However, within that broad category (juvenile seals) each of the annual stages is subject to many different influences. First-year survival may be affected by predation and maternal investment (i.e. wean mass) (McMahon *et al.* 2000), and the relative importance of these may be different at different islands (McMahon *et al.* 2003). Wean masses have increased in recent times at Marion Island (McMahon *et al.* 2003) which suggests that either food is more available or that young adult female mortality is relatively high. High mortality amongst young females would influence wean mass by generating a female age structure biased to older animals; and older females produce bigger, heavier pups (Arnbom *et al.* 1997; Fedak *et al.* 1996). Consequently the observed wean mass would likely increase. This would also suggest that food is limiting. However, as there has been a concurrent decrease in the age at first breeding, (McMahon *et al.* 2003) which is achieved through increased growth (Laws 1956b), it would seem unlikely that food is limiting. The amount of food available to the younger age classes at Marion Island would therefore appear to be sufficient. In fact, a recent increase in food availability within the Southern Ocean, as might be possible due to increase in ocean temperature (Gille, 2002), would provide a mechanism by which wean mass has increased. Because more food is available females grow faster and it would be expected that these faster growth rates would result in larger females that would produce larger pups.

Third-year survival may be limited by food availability, especially in females, as it is in the third year that many (39%) female seals become reproductively mature for the first time. In other mammals there is often a peak in mortality immediately following primiparity (Promislow 1991) and particularly so when food is limiting. Such resource limitations, while affecting all seals, are especially costly to younger elephant seal females (Reiter & LeBoeuf 1991) that suffer relatively greater mortality which ultimately reduces the number of recruits into the breeding population with the ultimate result of decreasing the net reproductive rate of the population (Sydeman & Nur 1994). Juvenile survival thus seems to be constrained by a number of direct intrinsic (physiological, e.g. growth), and extrinsic factors (food availability, predation) and some indirect factors such as the climate variability and its effect on food availability and competition for resources with other predators. These factors may of course also limit the fitness of adult seals but it can be anticipated that the effects would be reduced in adult seals because adult seals have

lower metabolisms and hence lower relative energy demands than younger, smaller seals (Bonner 1994; Boyd *et al.* 1994a).

Therefore, food availability can affect juvenile survival either indirectly by the amount of resources, in the form of blubber, a mother transfers to her pup during lactation (McMahon *et al.* 2000) and directly through increased mortality during food shortages. While a clear link has been established between wean mass (i.e. maternal foraging performance) and first year survival, the mechanisms describing how food availability affect survival in later years (second and third year survival) remains unclear. To be able to do this, the at-sea locations and behaviours of seals need to be determined. A limitation up to now on assessing the at-sea behaviour of predators like seals has been technology, most of which was based on archival data recorders that needed to be recovered to access the information stored within them. This was necessarily biased because the information that was gained from such studies was only represented by information from successful seals (surviving and returning to natal islands), while information on seals that died thus remained unknown. However, with the advent of more recent sophisticated technology that allows at-sea behaviour to be recorded and transmitted via satellite, the behaviour of both successful and unsuccessful animals can be determined (McConnell *et al.* 2002). These data will allow an interpretation of the requirements that seals need to survive. Indeed, such information also provides information on the strategies used by seals to cope with environmental fluctuations such as those caused by the Antarctic Circumpolar Wave (ACW) (Loeb *et al.* 1997; White & Peterson 1996) and the effects these processes have on survival.

Fate of the populations

The Macquarie Island seal population appears to have an overall negative intrinsic capacity for increase given that there were only a few years in which juvenile survival was maintained at the upper limit of the observed variation in survival. But while the probability of such an increase is low (3.4%) it can be borne in mind that this prediction is based on present demographic values. It does not preclude a different outcome given a change in any of these demographic parameters. Given this, it would seem prudent that the demographic study at Macquarie Island be continued to provide the stochastic model with more recent life-history parameters calculated from a longer time period. Such an extension of the project would comprise: (1) the continuation of the capture-mark-recapture program to determine variation in vital parameters (survival and fecundity) during large-scale environmental events such as the Antarctic Circumpolar Wave and (2) the inclusion of this variation in the stochastic model.

The Marion Island population, however, does not appear to have the demographic capacity to increase in the near future (several decades); and it appears headed for extinction unless there is either a dramatic change in the fundamental life-history parameters, such as improved adult female survival (Pistorius *et al.* 1999a) or some form of population supplementation. The observations on extinction times and extinction probabilities need to be treated cautiously. This is because our conclusions are drawn from models which cannot provide the reasons why populations are/have been behaving in a particular manner (Caughley 1994). Only integrated studies combining observational and experimental studies of life-history and ecology of a population can provide the more adequate of information needed to interpret and manage populations. Models make assumptions about the ecology of a particular species and also assume that currently measured/assessed mean trends remain constant. This, of course, is unlikely. The evidence presented here suggests that the Marion Island population may become extinct in the next 100-150 years. But, Marion Island experienced little immigration from proximate island colonies (Bester 1989; Condy 1978). However, neither the magnitude nor the effect of this migration has been quantified. Indeed, immigration to a small population, like the one at Marion Island, may contribute to a considerable change in the rate of population change similar to what was observed for northern elephant seals (Cooper & Stewart 1983).

Northern elephant seal populations have recovered from a small remnant population of approximately 20 individuals in the early 1890's to the present population of 127 000 (Bonnell & Selander 1974; Cooper & Stewart 1983; Stewart *et al.* 1994). These observations demonstrate that elephant seals do have the demographic capacity to recover after severe population depletions; and it indicates that there is potential for the Marion Island population to persist well beyond the times indicated here if foraging and immigration conditions alter. Indeed, when the Marion Island population was subjected to a small (four individual females) amount of immigration from a neighbouring colony I found that the probability of extinction decreased to 57%. Thus it seems that a low (but consistent) rate of immigration into the breeding population may have a dramatic effect on the persistence potential of a decreasing population such as the one at Marion Island. However, emigration of fecund females from Marion Island is also possible and has been reported (Guinet *et al.* 1992). Also, it might be suggested, that the rates of immigration and emigration could be equal, and so negate suggestions of net gain in the Marion Island population through migration. However, because constant immigration rates in all populations are unlikely and greater emigration from larger populations has been reported (Stewart & Yochem 1986; Stewart *et al.* 1994) it follows that larger populations probably act more often as source

populations. Therefore, positive net immigration is more likely at smaller populations such as Marion Island where more seals may arrive than leave. Immigration to Marion Island may be even more likely at Marion Island since the populations at the other island sites within the Kerguelen stock are said to be either stable or increasing (Guinet *et al.* 1999; Slip & Burton 1999) and may therefore be more likely to be source populations from which seals emigrate.

Significant changes in fecundity do not appear to affect rates of change in elephant seal populations (Bester & Wilkinson 1994; Bradshaw *et al.* 2002) but changes in survival do affect the geometric rate of population change (Bester & Wilkinson 1994; Hindell 1991). Our study and elasticity analyses support previous observations (Bester & Wilkinson 1994; Hindell 1991) that survival is the key demographic variable determining population growth rates. Furthermore, juvenile (ages 1-3) survival is the principal component driving the growth rates contributing to the total population growth rates of elephant seals. This is consistent with previous observations at Macquarie Island (Hindell 1991) while contrasting others (Galimberti & Boitani 2001; Pistorius & Bester 2002a; Pistorius *et al.* 1999b) who dealt with the small populations at Marion Island and the Falkland Islands respectively. They concluded that adult female survival was the key factor controlling population persistence. Recent reviews (Benton & Grant 1999; Benton *et al.* 1995; Gaillard *et al.* 1998) of long-term demographic studies of large herbivores generally showed that survival and not fecundity had the greatest impact on population growth. However, in these studies of herbivores there was some uncertainty as to the relative importance of juvenile survival (recruitment) and adult survival on population growth. It was recognized that both vital rates may at times be more important, or equal, in the determination of population growth rates (Benton & Grant 1999).

One of the foremost findings from these analyses was that the vital rates at Marion and Macquarie islands were broadly similar, but the small differences in these vital parameters between these islands had potentially large impacts on population growth rates. If small changes in population parameters are going to be used with any precision in estimating future population sizes, the errors associated with the estimates need to be small and thus long time series are needed. The longer the series, the more accurate the model results in predicting future population sizes. Indeed, stochastic models such as the one used here are a valuable tool to manipulate populations under various theoretical conditions (Reed *et al.* 2002) and in so doing can provide useful insights for the management of endangered populations (Engen *et al.* 2001). Models, however, are not perfect representations of reality and should be used cautiously and with some form of validation and confidence measure (McCarthy & Broome 2000; McCarthy *et al.* 2001a).

It can be concluded that while PVAs are valuable tools for predicting population trajectories, (Brook *et al.* 2000) their value is limited by two assumptions: (1) that the distribution of the vital rates are constant between years and individuals and (2) that changes in these rates may be readily detected (Coulson *et al.* 2001). This was the case for our estimates as the model was able to predict population sizes accurately in the short-term when little variation in vital rates such as survival is known to occur (Pistorius *et al.* 1999a); but predictions in the longer term were unreliable where variation in vital rates such as survival has been documented (Hindell 1991; McMahon *et al.* 1999).

Chapter - 6 Southern elephant seals: a review of current population sizes and population changes

Introduction

The southern elephant seal (*Mirounga leonina* Linn.) is one of the more numerous pinniped species in the world and much research and scientific interest have been focussed on this animal. This was largely due to the accessibility of the seals to researchers and the predictability of the haulout and breeding behaviour of the seals; the same reasons that made the seals attractive to earlier exploitation by sealers. Initially the contact between humans and seals was one of exploitation by man. Elephant seals were seen entirely as an economic resource of high quality oil derived from their blubber deposits. This attitude was current at all their major breeding grounds. Economic utilization of the seals for their oil greatly reduced many populations (Busch 1985). However, a decrease in the world market of seal oil and the near extinction of the commercial trade in fur seal skins (Bonner 1989; Busch 1985) resulted in the abandonment of much of the elephant seal hunt. This allowed most populations to recover in the last decades of the 19th century (Bonner 1989; Laws 1994).

Southern elephant seals have a circumpolar distribution and four distinct population stocks are recognized: the Peninsula Valdés stock in Argentina, the South Georgia stock in the south Atlantic Ocean, the Kerguelen stock in the south Indian Ocean and the Macquarie stock in the south Pacific Ocean (Hoelzel *et al.* 2001; Slade *et al.* 1998). The principal breeding colonies for these stocks are located on: Peninsula Valdés, South Georgia Island, Heard Island and Îles Kerguelen, and Macquarie Island respectively (Fig.1.1).

Here I summarize the current knowledge on the status of each stock and assess recently acquired information to review and compare these distinct populations. Reports (Burton 1986; Condy 1978; Condy 1984; Hindell & Burton 1987; van Aarde 1980a) of large decreases in the Indian and Pacific Ocean elephant seal populations during the 1980s prompted a number of research initiatives to discover the reasons for these decreases in a major Antarctic marine predator. Accompanying these discoveries of precipitous population decreases was a shift in research focus from studying and understanding fundamental biological parameters such as reproductive and behavioural biology, to studying primary ecological parameters such as survival and foraging ecology (Hindell *et al.* 1994b; Laws 1994). Such decreases in the numbers of an apex vertebrate predator caused concern because these changes were seen as perhaps indicating larger unrecognized ecosystem changes. Such new research (Bester & Wilkinson 1994; Hindell *et al.*

1991a; Hindell *et al.* 1991b; LeBoeuf *et al.* 2000; Slip *et al.* 1994) included the establishment of long-term demographic studies to quantify seal life-history parameters and the deployment of newly developed archival dive recorders and satellite telemetry systems to study population demography and at-sea foraging. The fruits of these research initiatives have recently become available and now allow for the: (1) re-assessment of the world wide status of southern elephant seals, (2) comparison of populations (3) re-examination of previously postulated hypotheses on population decreases and (4) postulation of some new hypotheses and directions for future research.

Southern elephant seal numbers

Three distinct populations or stocks have been recognized with the possibility of a fourth (Laws 1994). Contemporary studies have recently confirmed the existence of four distinct populations with little or no permanent female migration between populations (Hoelzel *et al.* 2001; Slade *et al.* 1998). Of the four populations, the South Georgia Island population is numerically the largest, followed by the Heard Island and Îles Kerguelen populations, Macquarie Island, and Peninsula Valdés populations (Table 6.1). Together these five island populations account for ~98% of the total population. The remaining 2% of the elephant seal number are made up of small populations scattered throughout the sub-Antarctic and adjoining regions (Fig. 1.1). These populations occur on the: Prince Edward Islands, Gough Island, Îles Crozet, Campbell Island, Antipodes Islands, South Orkney Islands, South Shetland Islands, South Sandwich Islands, the Falkland Islands and Bouvetøya (Laws 1994). In addition to these regularly breeding populations there have been reports of isolated births in Antarctica, (McMahon & Campbell 2000; Murray 1981) in Tasmania (Pemberton & Skira 1989; Tyson 1977, personal observation¹ and Fiona Hume, personal communication²), Australia (Mawson & Coughran 1999), South Africa, and on Tristan da Cunha, St Paul Island and Amsterdam Island (Laws 1960).

¹ A single female pup was born on Dover Beach on the 25th October 2000 and successfully weaned 22 days later on 16th November 2000, when she weighed 85.5kg, had a length of 1.30m and a girth measurement of 1.10m.

² Two weaned pups were observed in November 2000 on Maatsyker Island

Table 6.1. The estimated population sizes of southern elephant seals in 2001.

Population (Stock)	Location	Population Size	Reference	Change (1990-present)
South Georgia	South Georgia	397 054	(Boyd <i>et al.</i> 1996)	Stable
	South Orkney Is	20	(Laws 1994)	Unknown
	South Shetland Is	2 300	(Laws 1994)	Unknown
	Falkland Is	1 827	(Galimberti & Boitani 1999)	Stable
	Gough Is.	63	(Bester <i>et al.</i> 2001)	Decrease
	Bouvetøya	308	(Kirkman <i>et al.</i> 2001)	Increase?
<i>Stock total</i>		<i>401 572</i>		
Kerguelen	Îles Kerguelen	153 237	(Guinet <i>et al.</i> 1999)	Stable
	Heard Is	61 933	(Slip & Burton 1999)	Stable
	Marion Is	1 405		Decrease/Stable
	Prince Edward Islands	Unknown		
	Îles Crozet & Possession Is	1 995	(Guinet <i>et al.</i> 1999)	Stable
	<i>Stock total</i>		<i>218 570</i>	
Macquarie	Macquarie Is	76 000		Decrease
	Antipodes Is	249	(Anonymous 2001)	Decrease
	Campbell Is	<10		Decrease
<i>Stock total</i>		<i>76 259</i>		<i>Decrease</i>
Peninsula Valdés	Peninsula Valdés	42 371	(Lewis <i>et al.</i> 1998)	Increase
<i>Stock total</i>		<i>42 371</i>		<i>Increase</i>
Total world population		738 772		Increase?

The South Georgia Stock

This stock includes populations at: South Georgia Island, the Falkland Islands, South Orkney Islands, King George Island, Nelson Island, Avian Island, the South Sandwich Islands, Gough Island and Bouvetøya. The South Georgia Island population is the single most numerous element (397 054) and is the most significant one (>99%) of this stock. It comprises approximately 54% of the global population (Boyd *et al.* 1996). This population, and hence the stock, has remained stable since 1951 (Boyd *et al.* 1996; McCann & Rothery 1988). It has been suggested that this stability may be due to the elephant seal population in this zone being buffered against ecosystem and environmental change that affected their food supply. However this hypothesis was negated in the light of evidence from other higher predators at South Georgia Island (Boyd *et al.* 1996).

The Falkland Islands support a small population of elephant seals on Sea Lion Island that have been censused irregularly and of which little is known (Laws 1960; Laws 1994). However, recently an ecological program researching the elephant seals at Sea Lion Island has been established (Galimberti & Boitani 1999). Adult mortality rates were (deemed) the most important factor affecting extinction risk and although the population does not appear to be at immediate risk of extinction, further study is advised (Galimberti & Boitani 2001). This study has shown that: (1) the total population on Sea Lion Island is 1 800 seals and (2) that breeding is restricted to this single location (Galimberti & Boitani 1999). This population appears to have increased rapidly from very few seals at the end of sealing at the Falkland Islands to approximately 3 500 in the 1950s (Laws 1960), and after a subsequent drop appears to have again stabilized since 1989 (Galimberti & Boitani 1999; Galimberti & Boitani 2001). Presently this population is placed within the South Georgia Stock (Laws 1994). There is little evidence of migration between the Sea Lion Island and Peninsula Valdés populations (Galimberti & Boitani 1999; Lewis *et al.* 1996) and between the Sea Lion Island and South Georgia populations (Sanvito & Galimberti 2000); and therefore it has been suggested (Hoelzel *et al.* 2001) that there is little gene flow between these populations. This evidence needs to be treated cautiously because only few animals were marked at any of these locations (Arnbom *et al.* 1997; Galimberti & Boitani 1999; Lewis *et al.* 1996) and only a few breeding animals are needed to link the populations genetically (Slade *et al.* 1998).

Acoustic studies of male vocalisations have shown that geographic variations exist between sites at the Falkland Islands and Peninsula Valdés (Sanvito & Galimberti 2000). This would suggest that these populations are reproductively isolated and therefore may even possess a slightly

different genetic identity to the Falkland Islands population. Such differences in vocalizations have been termed cultural differences (Sanvito & Galimberti 2000) and it is believed that these cultural differences may indeed facilitate population differentiation through ecological isolation (Schulter 2001). Unfortunately, information from other locations are at present not available for comparison and hence the significance (in terms of population structure) of these differences cannot be evaluated (Sanvito & Galimberti 2000). Given the cultural difference between the Falkland Islands and Peninsula Valdés populations that are ~1 150 km apart one may expect a similar difference between the Falkland Islands and South Georgia populations that are ~1 400 km apart. But whether these differences equate to “stock-level” differences remain unknown. Further genetic research would be necessary to decide this. However, there appears to be some evidence for cultural differences between the Falkland Islands and South Georgia populations. Such differences may, in the short term, promote insularity and therefore enhance ecological differences between populations. Hence, in a management sense it is prudent to consider these populations as ecologically unique entities that require population specific management actions.

The Kerguélen Stock

Five island populations constitute this stock: Îles Kerguélen, Heard Island, Marion Island and Prince Edward Island, and the Îles Crozet and Îles Possession. The breeding populations on Îles Kerguélen and Heard Island account for 97% of this stock. All these populations showed evidence of dramatic decreases of ~50% since the 1950s (Barrat & Mougin 1978; Bester 1988; Bester & Lenghart 1982; Bester & Wilkinson 1994; Burton 1986; Pistorius *et al.* 2000; van Aarde 1980a) but, recently some of these populations are thought to have stabilized (Guinet *et al.* 1999; Pistorius & Bester 2002a; Pistorius *et al.* 2001; Slip & Burton 1999).

Between 1952 and 1979 the population at Îles Kerguélen may have decreased on two occasions, the first between 1956 and 1960, and again between 1970 and 1977, although there are no data for the period 1960 to 1970 (Pascal 1986). There has been an overall decrease of 44% from 1956 to 1989 at Îles Kerguélen and an apparent period of stability from 1984 to 1989 (Guinet *et al.* 1992). This “stability” has not been tested by robust methods of trend analysis; but if true it suggests that in recent times the factor/s responsible for the earlier decreases may have ameliorated (Guinet *et al.* 1999).

The population at Heard Island has received little study. A decrease in the population of approximately 47% from 1949 to 1985 has been reported (Burton 1986), but any attempts at

explaining this decrease (Hindell *et al.* 1994b) have relied largely on information gained from studying other populations. Evaluating and interpreting the status of the Heard Island population is important because it constitutes about 30% of the Kerguelen stock and about 9% of the world population of southern elephant seals (Laws 1994). Recently Slip & Burton (1999) concluded that the Heard Island population had remained stable between 1985 and 1992. This (Slip & Burton 1999) was attributed to an increase in the sea-ice extent (de la Mare 1997) and a corresponding increase in food availability. If correct, this lends support to the view that large scale environmental changes have caused many of the post-sealing decreases in elephant seal populations.

At Îles Crozet the population decreased at an annual rate of 5.75% between 1966 and 1976, (Barrat & Mougín 1978) and continued to decrease at 5.70% per year from 1980 to 1989 with an overall decrease in the population of 70% from 1966 to 1989 (Guinet *et al.* 1992). However, this rapid decrease in numbers has been from a small population (1 995 or 0.27% of the world population) which does intermix with that of Kerguelen itself. It is well known that elephant seals can redistribute themselves rapidly between close island groups (Bonnell & Selander 1974; Stewart *et al.* 1994). Guinet *et al.* (1999) judged that the population at Îles Crozet had remained stable between 1990 and 1997 with no significant change in the number of breeding females counted between 1990 and 1997. The possibility of migration between islands in relatively close proximity (1 283 km) cannot be excluded and the change in the rate of population decrease at Îles Crozet may conceivably be due to an influx of immigrants from a source population such as Îles Kerguelen where the population is believed to be increasing (1.1% *pa*) (Guinet *et al.* 1999).

The Marion Island population showed a similar large decrease of 69.5% from 1951 to 1986 (Wilkinson & Bester 1988). The population decreased at a rate of 4.8% per annum between 1974 and 1989 but then apparently slowed to 1.9% per annum between 1983 and 1989 (Bester & Wilkinson 1994). A recent analysis of the population trends at Marion Island (Pistorius *et al.* 1999b) concluded that the population decreased at an annual rate of ~4.3% from 1986-1991 but this rate slowed to 2.5% between 1991 and 1997. This conclusion is based on only six years of data gathering and may be premature as previously shown (Bradshaw *et al.* 2002).

The long-term demographic study at Marion Island (Bester 1988) has provided insights into the mechanisms and pertinent demographic parameters that drove the decrease of the Marion Island population (Pistorius *et al.* 1999a; Pistorius *et al.* 1999b; Pistorius *et al.* 2001). It was found that: (1) adult survival rates had increased and that the previous lower survival was one part of the

population decrease and (2) fecundity was an early demographic parameter which responded to environmental or population change (Pistorius *et al.* 2001). However, it was determined that: (1) changes in fecundity had a relatively small impact on the rate of population change (Bester & Wilkinson 1994), and (2) whether there was a statistically detectable change in the rate of population decrease at Marion Island (Bradshaw *et al.* 2002) in recent times remains a moot point.

The Macquarie Stock

Only three island populations make up this stock namely: Macquarie Island, Campbell Island and the Antipodes. However, this stock is virtually confined (99%) to Macquarie Island; and as such, the discussion of this stock will centre on the status and change of the Macquarie Island population. This elephant seal stock is one of the most continuously studied populations (Carrick & Ingham 1962b; Hindell 1991; Hindell *et al.* 1994b; McMahon *et al.* 2000). The population at Macquarie Island has decreased by 59% from approximately 183 000 in 1949 (Hindell & Burton 1987) to approximately 76 000 at present (AAD records). This represents a severe decrease in the major constituent of the stock that remains largely unexplained. However, there has been a recent amelioration in the annual rate of decrease from 2.1% between 1949 and 1985 (Hindell & Burton 1987) to 1.7% per annum between 1985 and 1998 (AAD records).

The single most important aspect of the decrease in seal numbers at Macquarie Island was the dramatic decrease in first-year survival during the early 1960s to below 2% in 1965 while post one-year survival remained constant (Hindell 1991). It was suggested that changes in the Macquarie Island population since the 1960s were largely attributable to the subsequent low rates of recruitment into the population (Hindell 1991). This evidence, of decreasing first-year survival and constant post one-year survival from the 1950s to the 1960s, would suggest that first-year seals are different to post one-year seals with respect to diet and foraging areas and their ability to access and exploit distant foraging grounds. Therefore, elucidating the factors important in the survival of first-year seals should provide evidence that would explain the decrease in seal numbers (Hindell *et al.* 1994b). There has been a growing body of information describing the behaviour and survival of first-year seals (Bell *et al.* 1997a; Hindell *et al.* 1999; Irvine *et al.* 2000; McMahon *et al.* 1999; McMahon *et al.* 2000). These studies have shown that elephant seals in their first year of life do indeed behave differently at sea (Hindell *et al.* 1999; Irvine *et al.* 2000), utilize different foraging grounds (Hindell *et al.* 1999) and that their survival is influenced by their wean mass (McMahon *et al.* 2000). Although these studies have highlighted the differences

between adult and juvenile seals (Hindell *et al.* 1999; Irvine *et al.* 2000) it also accentuated the dependence of juvenile survival on maternal investment (McMahon *et al.* 2000) and hence maternal (adult) foraging success (Arnbom *et al.* 1997; Fedak *et al.* 1996). It would then seem unlikely that first-year (juvenile) survival alone would be responsible for the dramatic decreases in seal numbers but that adult survival and the ability of adults (female) to provision their young had also contributed to the decreases. Therefore, a factor affecting both juveniles and adults seems likely to have caused the observed decreases. Such a factor may be environmental change because it can conceivably affect juveniles and adults equally. Nonetheless, the mechanisms are likely to be different. Juvenile seals would be affected in two ways by a negative environmental anomaly: (1) indirectly by having poor fat stores (derived from their mothers) when they embark on their first foraging trips and (2) directly by being unable to locate and procure prey and thus suffering increased mortality. The outcome in terms of population growth though is the same as it results in low recruitment rates. Adult female seals too could be affected in different ways by food unavailability: (1) they suffer greater mortality, although this appears to be unlikely from earlier studies (Hindell 1991) and (2) they face lower fecundity (Pistorius *et al.* 2001; Stanganelli & Vergani 2000).

The Peninsula Valdés Stock

This stock has only recently been recognized as a distinct stock (Hoelzel *et al.* 2001; Slade *et al.* 1998) although there have been earlier suggestions for this (Laws 1994). Peninsula Valdés is the only continental breeding population at present, all the others being restricted to remote oceanic islands. However there are historical records of continental breeding colonies in South Africa (Ling & Bryden 1992). Of all the Southern Hemisphere elephant seal populations, this population has increased in size for longer than any other in recent times (Campagna & Lewis 1992; Laws 1994) and continues to increase (Lewis *et al.* 1998). Pup production at Peninsula Valdés has increased by 41% between 1982 and 1997 (Lewis *et al.* 1998). This increase could have occurred as a result of: (1) immigration from other sites or (2) an increase in breeding females as a result of intrinsic population growth (survival of females). Female immigration does not occur (Hoelzel *et al.* 2001) which suggests that the increases in population size are likely to be due to high female survival (Pistorius *et al.* 1999a; Pistorius *et al.* 2001; Pistorius *et al.* In review). Such high female survival may conceivably result from adequate or increasing resource availability.

Population change hypotheses

Many hypotheses have been presented in an attempt to describe the precipitous decreases in some elephant seal populations and the apparent stability of other populations during the past 50 years (1950s – 2000). These hypotheses fall into two broad categories, the intrinsic (density dependent) model and the extrinsic (density independent) model. The intrinsic model includes factors that are affected by density dependent mechanisms such that effect increases with increased numbers of seals. Included in the intrinsic model were: the paucity of male hypothesis (Skinner & van Aarde 1983), the overshoot hypothesis (Hindell 1991; Hindell *et al.* 1994b), a density dependent mechanism (Reiter *et al.* 1978; van Aarde 1980b) and the pandemic disease model (Harwood & Hall 1990). The extrinsic models included the predator model (Condy *et al.* 1978; Guinet 1992a; Guinet 1992b), fisheries competition model (Pascal 1986), inter-specific competition model (Hindell *et al.* 1991a) and the environmental change model (Burton 1986; Hindell *et al.* 1994b).

Intrinsic models

Male paucity

In an attempt to describe the reasons for the decrease in numbers of the Marion Island population a hypothesis was proposed that suggested a scarcity of sub-ordinate adult males was implicit in the decrease (Skinner & van Aarde 1983). Skinner & van Aarde (1983) suggested that there were fewer sub-ordinate male elephant seals at Marion Island than at Îles Kerguelén. These authors then hypothesized that a significant number of female seals at Marion Island leaving the breeding harems, after weaning their pups, were not pregnant, because there were not enough sub-ordinate males to mate with them. This short-fall of males hypothesis predicted that despite the polygynous nature of elephant seals during breeding, harem masters (dominant males) were unable to either successfully mate with all the cows in their harems and/or that they were not successful at inseminating all the females that they mated. The sub-ordinate males thus provided a secondary mechanism to ensure insemination that was absent at Marion Island. The implication here is that low sexual vigour of harem masters (low rates of mating and insemination) may be contributing to the decreases observed here and at other elephant seal colonies, a notion that was challenged by both Bester & Wilkinson (1994) and Pistorius *et al.* (1999). To test this hypothesis of Skinner & van Aarde (1983), Wilkinson & van Aarde (1999) investigated three aspects of elephant seal breeding behaviour: (1) adult sex ratios, (2) male sexual activity and (3) the relationship between male sexual activity levels in one year (t) and the probability of female pupping in the following season ($t + 1$), i.e. male fertility. This study (Wilkinson & van Aarde

1999) found that: (1) adult sex ratios at Marion Island were similar to those at other sites where populations were both stable or increasing, (2) harem masters were capable of high rates of sexual activity mating with all the females present during the breeding season and (3) harem masters were fertile and had high rates of conception. The male paucity hypothesis was thus rejected and it was concluded that other mechanisms be sought to explain the decrease in the Marion Island population. Consequently, it appears that male paucity is not contributing to decreases in this and other southern elephant seal populations.

Overshoot hypothesis

This hypothesis states that the decreases in southern elephant seal populations around the globe were a direct result of the eighteenth and nineteenth century exploitation of seals (Hindell 1991; Hindell *et al.* 1994b) during which time elephant seal populations were reduced well below pre-sealing levels (Hindell & Burton 1988a). This low abundance of elephant seals enabled elephant seal prey species to increase during the sealing era allowing for an abundant resource at the end of exploitation. Elephant seal populations were thus enabled, in the presence of “limitless” resources, to increase in numbers such that the pre-sealing population numbers were “overshot”. The subsequent decrease in seal populations is therefore a consequence of the over-exploitation of existing food resources and a shift to a smaller and sustainable population level. This hypothesis was developed because it appeared to account for some of the characteristics of the observed population decreases such as the differences between that stability of the South Georgia population and the negative instability of the Kerguelen and Macquarie populations. Managed sealing (exploitation) continued at South Georgia for much of the twentieth century whilst it was abandoned at Îles Kerguelen and Macquarie Island. It was suggested that this managed exploitation of the adult component of the South Georgia population maintained the population at a sustainable pre-sealing level but, this was exceeded in the Kerguelen and Macquarie stocks such that once abundant food resources were overexploited and became inadequate to sustain the growing populations (Hindell *et al.* 1994b). The populations in the Kerguelen and Macquarie stocks thus began to decrease because of an increase in juvenile mortality (Hindell *et al.* 1994b) as recorded in the mid-1960s (Hindell 1991). Further support was lent to the overshoot hypothesis because both the male and female components of the population decreased simultaneously and at similar rates, suggesting that the factor(s) driving the decrease acted on seals prior to the development of the sex differences in morphology and behaviour. Adult male and female elephant seals grow at different rates (McLaren 1993), forage in distinct locations (Slip *et al.* 1994) and behave differently when at sea (Hindell *et al.* 1991b; McConnell *et al.* 1993; Slip *et al.*

1994), whilst juvenile seals do not exhibit these sex differences (Bell *et al.* 1997a; Hindell *et al.* 1999; Irvine *et al.* 2000; Slip 1997a).

This hypothesis assumes: (1) a simple predator-prey relationship and (2) that southern elephant seal prey was not exploited by other non-harvested predators, such as whales and fish. Only under these conditions could the prey species increase in numbers as proposed in the overshoot hypothesis (Hindell 1991). However, the hypothesis has several problems to deal with. Firstly, the existence of a simple predator-prey relationship is unlikely because elephant seals take diverse fish and squid prey species (Burton & van den Hoff 2002) and complex relationships can exist for seals with even simple diets (Yodzis 2000; Yodzis 2001). Therefore, the assumption of a simple relationship seems unlikely. Furthermore, the diet of the southern elephant seal consists of squid and fish of somewhat similar size and composition to those consumed by the southern bottlenose whale (*Hyperoodon planifrons*). This suggests that southern bottlenose whales and other beaked whale species can compete for prey with elephant seals (Slip 1995; Slip *et al.* 1995). Thus competitors do exist and their possible effects on food resources and food web structure make the simple overshoot hypothesis unlikely. Secondly, this hypothesis has been proposed as a concept but there is no direct evidence to support it. The prey items of southern elephant seals (Burton & van den Hoff 2002) are fast growing animals and no data exists to show the hypothesised long-term changes in their abundance over time. Future studies describing the diet composition of potential food competitors will no doubt provide valuable information that will allow comparisons and the assessment of the level of competition between elephant seals and whales. But given the present state of knowledge, it seems unlikely that elephant seals do not have food competitors.

Pandemic diseases

It has been suggested that disease may act in regulating pinniped populations (Harwood & Hall 1990; Visser *et al.* 1991). Indeed, disease outbreaks cause mass mortalities in many pinnipeds with dire consequences for small or endangered seal populations (Kennedy 1998; Kennedy *et al.* 2000; Osterhaus *et al.* 1997; Osterhaus *et al.* 1998; van de Bildt *et al.* 1999). Despite this growing body of evidence that has isolated many viral agents from mortality events there is no evidence of widespread disease in southern elephant seals. However, in a recent study, Linn *et al.* (2001) have isolated and discovered a novel alpha-virus in the host specific, blood sucking southern elephant seal louse, *Lepidophthirus macrorhini*. All of the seals examined in this study were sero-positive and had neutralizing antibodies against the virus. Infection occurred early in life and persists throughout the life of the seal (Linn *et al.* 2001). However, no virus-related pathology was

identified. Also, there have been no reports of numbers of sick or dead southern elephant seals occurring on island beaches. At Macquarie Island the scientific station is only ~50 m from a large (~3000 adult female) breeding and moulting beach of southern elephant seals. The station has been continuously manned for >50 years and seal observers have kept account of the seal numbers (Carrick & Ingham 1962b) through the period of greatest decrease. Seal numbers dropped but no signs of illness or very poor condition seals were seen. A mortality event of similar severity to the recent North Sea seal distemper would have been very likely to provide carcasses and visibly afflicted seals. Although no pathology was associated with the new virus from Macquarie Island, its existence (Linn *et al.* 2001) does highlight the deficiency in our knowledge of seal pathogens and their possible effects on seal populations, particularly in the Southern Hemisphere. These effects of viral infections may not always be manifested in dramatic mass mortality events as observed in the Northern Hemisphere (Kennedy *et al.* 2000; Osterhaus *et al.* 1997; van de Bildt *et al.* 1999) but may be subtle and difficult to detect. This is particularly relevant to seals because they spend most of their lives as pelagic marine predators when it is arduous to observe or study them. The role of disease in pinniped population regulation is therefore complex and needs to be addressed to fully assess the effect of pathogens of seals before being rejected as a regulatory agent.

Extrinsic models

Predation

One factor common to all four stocks of elephant seals is the presence of killer whales, *Orcinus orca*, offshore from their breeding sites when weanlings are first entering the sea. Predation by killer whales has been suggested as a factor in the decrease of the southern elephant seal populations at Marion Island and at Îles Crozet (Condy *et al.* 1978; Guinet 1992b). At Île de la Possession observed predation by killer whales on weaned pups was 25% on one beach, however, the actual predation was probably higher (Guinet 1992b). Killer whales are rarely sighted off Heard Island (Australian Antarctic Division, unpublished data) and in the Kerguelen Archipelago (Guinet 1992b). They occur in relatively small numbers around South Georgia Island (Headland 1984) and Macquarie Island (Copson 1994). Thus, there appears to be some evidence suggesting that predation by killer whales acts more strongly or is more visible on small populations (Trites *et al.* 1997) such as those at Marion Island and at Île de la Possession (Condy *et al.* 1978; Guinet 1992b) where killer whales occur in relatively high numbers. However, because these island populations are small and constitute less than 1% of their respective stocks it seems improbable

that predation played(s) a significant role in the global decreases in elephant seal populations, although there may be a strong local effect.

Fisheries competition

Several authors have suggested that depletion of marine resources by commercial fisheries may have been responsible for the decrease of Indian Ocean elephant seal populations (Pascal 1986; van Aarde 1980a; Wilkinson & Bester 1988). The main stocks of fish on the Kerguelen shelf were reduced through heavy unregulated fishing effort (Duhamel & Hureau 1990), and the decrease of elephant seals at Îles Kerguelen between 1970 and 1980 corresponded to this period of unregulated exploitation which lent support to the view of fisheries causing the decreases in numbers. However, fish stocks at South Georgia also decreased (Kock *et al.* 1985) without any noticeable effect on the elephant seal population there. Moreover, the Macquarie Island elephant seal population decreased from the 1950s - 1990s with no fishing having occurred in that region nor in the pelagic areas identified as the principal foraging grounds of the Macquarie Island seals (Hindell *et al.* 1991b; Slip *et al.* 1994). This together with the observations at South Georgia would indicate that competition with fisheries is not a cause implicated in the global decrease of elephant seals.

Recent studies of the diet of elephant seals (Burton & van den Hoff 2002; Daneri *et al.* 2000; Green & Burton 1993; Rodhouse *et al.* 1992; Slip 1995) have shown that there is little or no overlap between the species eaten by elephant seals and those caught in any of the historic or existing fisheries in the Southern Ocean. However, these observations must be treated cautiously because (1) the predator-prey relationships are likely to be complex and (2) extrapolating from direct observations may be misleading through underestimating the complexity of the relationships (Yodzis 2001). Furthermore, this interpretation is tentative because diet assessments through lavage only represent the recent diet of elephant seals (Krockenberger & Bryden 1994) and may not be representative of their pelagic diets at distant foraging grounds.

Inter-specific competition

Competition between elephant seals and other faunal taxa in the Southern Ocean can take two forms: (1) direct or indirect competition for food resources and (2) direct or indirect competition for haulout (breeding and moulting) areas.

Competition for food

The southern bottlenose whale is a major consumer of cephalopods and, while in Antarctic waters, it can feed on essentially the same squid species that have been found in some elephant

seal stomachs (Sekiguchi *et al.* 1993; Slip 1995). The mean sizes of most prey species common to both were also similar (Slip 1995; Slip *et al.* 1995). Thus the southern bottlenose whale is a potential competitor with the southern elephant seal as might be other ziphiid odontocetes. The summer population of ziphiid whales in Antarctic waters has been estimated at between 224 000 and 377 000 (Sekiguchi *et al.* 1993) which represents considerable potential competition for squid resources with the southern elephant seal. However, it is unknown how much foraging time these whales spend in Antarctic waters. Further studies of diet and temporal and spatial distribution patterns of ziphiid whales may provide insights into how much over-lapping temporal and geographic competition they might provide for southern elephant seals. Further, concurrent diet studies of king penguins, *Aptenodytes patagonicus*, and elephant seals at Heard Island (Moore *et al.* 1998; Slip 1995) show some overlap in the prey items, particularly squid and predominantly in the austral winter, consumed by these two taxa. Dietary overlap between elephant seals and king penguins has also been recorded in a study at Îles Kerguelen (Cherel & Weimerskirch 1999). But, this needs to be treated cautiously because although there is an overlap in prey items no temporally comparative data are available on prey size and diet composition, which therefore limits direct comparison between groups. However, recent diet information collected from stranded cetaceans and pinnipeds suggests considerable overlap in the squid portion (especially Ommastrephidae) of the diets of the larger odontocete whales (*Orcinus orca*, *Pseudorca crassidens*, *Kogia breviceps*, *K. sima* and *Physeter macrocephalus*), fur seals (*Arctocephalus gazella*, *A. tropicalis* and *A. australis*) and elephant seals (dos Santos & Haimovici 2001; Santos *et al.* 2001) despite the apparent differences in depths at which these groups forage (Boyd & Arnborn 1991; Boyd *et al.* 1994b; Costa *et al.* 1989; Georges & Guinet 2000; Georges *et al.* 1999; Hindell *et al.* 1991b; McCafferty *et al.* 1998; Moore *et al.* 1999; Schreer *et al.* 2001). A recent contribution (Barlow *et al.* 2002) to this debate concluded that Antarctic fur seals (*Arctocephalus gazella*) and macaroni penguins (*Eudyptes chrysolophus*) were probably feeding on the same populations of krill around South Georgia, despite the segregation of size of krill eaten by the two species, and was unable to provide direct evidence for or against competition between these two taxa. The extent to which inter-specific competition in the Southern Ocean affects various taxa including elephant seals is, however, reliant on determining the food web relationships, which are poorly understood.

Competition for haulout areas

The beach areas of the sub-Antarctic islands on which elephant seals breed and moult are also areas that are utilized by many other Southern Ocean predators including: Antarctic fur seals, sub-Antarctic fur seals *A. tropicalis*, king penguins, macaroni penguins and royal penguins *E.*

schlegeli. Competition for this limited haulout space can be fierce especially in those situations where dramatic increases in the populations of fur seals and king penguins have occurred (Boyd *et al.* 1995; Chamaille-Jammes *et al.* 2000; Hofmeyr *et al.* 1997; Shaughnessy *et al.* 1998; Woehler & Croxall 1997). The actual mechanism by which this competition could affect elephant seal populations is not known as elephant seals are large and not easily disturbed (Burton & van den Hoff 2002). However, populations of these possible “space competitors” are increasing in all/most locations where elephant seals occur but only at Macquarie Island is the elephant seal population still decreasing (Burton unpublished data). This suggests that it is very unlikely that competition for space is an explanation for the observed widespread decreases in elephant seal numbers. Further, the temporal difference in breeding and moulting times of these taxa, and the slightly different habitats used during the breeding season haulout in particular (Hindell & Burton 1988b; Kerley 1983; Weimerskirch *et al.* 1992) provide additional information refuting the hypothesis of competition for space on land.

Environmental change

Another possible explanation is that the decreases in seal numbers are due to changes in the ocean environment that has had an impact on the food of the southern elephant seal (Burton 1986; Burton *et al.* 1997; Hindell *et al.* 1994b; McCann & Rothery 1988). However, southern elephant seals forage widely throughout the Southern Ocean and some animals from different stocks may even use the same foraging areas. The eastern limit of the range of the South Georgia stock overlapped with the western limit of the range of the Kerguelen stock, the eastern limit of the range of the Kerguelen stock overlapped with the western limit of the range of the Macquarie stock and the northern limit of the range of the South Georgia and southern range of the Peninsula Valdés stocks foraging grounds overlapped (Bester & Wilkinson 1994; Campagna *et al.* 1995; Campagna *et al.* 1998; McConnell & Fedak 1996; Slip *et al.* 1994). Thus, any profound environmental change to broad areas of the Southern Ocean might at first sight be expected to affect all populations of southern elephant seals that can range widely. However, it seems that although individual seals may forage widely most share common foraging areas (Hindell *et al.* 1991a; Jonker & Bester 1998; McConnell & Fedak 1996; McConnell *et al.* 2002; Slip *et al.* 1994; van den Hoff *et al.* 2002).

Recently de la Mare (1997) reported that a decrease in Antarctic sea ice occurred relatively quickly beginning in the mid-1950s and ending by 1973. This decrease was of about 2.8° of latitude averaged from October to April, and suggests a reduction of about 25% of sea ice (de la Mare 1997). The marginal sea-ice edge is also an area of enhanced biological productivity (Smith

& Nelson 1985a; Smith & Nelson 1985b). Prior to the mid-1950s and since 1973 the sea-ice has remained stable, but the decrease of sea-ice in the intervening period suggests that a decrease in productivity of the Southern Ocean ecosystem may have occurred because the marginal sea-ice zone plays an important role in primary production (de la Mare 1997). The time scale of this environmental change corresponded with the observations of decreases in elephant seal numbers. Unfortunately, there are gaps in both the sea-ice data and particularly in the elephant seal data in the period 1960-1970, which make it difficult to correlate the changes. However, the sea-ice appears to have been stable then decreased by about 25% over approximately a decade during the 1960s and then returned to a stable system (de la Mare 1997). Elephant seal numbers at Heard Island, and Îles Kerguelen, have followed a similar pattern with possible recent stabilizations of the seal populations at these locations (Guinet *et al.* 1999; Slip & Burton 1999). These observations thus can link large-scale environmental change to the decreases in seal numbers. However, it does not explain adequately the continued decrease in numbers at Macquarie Island, the stability of the South Georgia stock and the increases in the Peninsula Valdés stock. It is pertinent to note that only populations in the southern Indian and southern Pacific Oceans have decreased whereas the populations in the southern Atlantic Ocean have remained stable or increased. It is clear that there has been no one regular forcing of a global nature driving the decreases as the southern Atlantic populations have not been affected whilst the Indian Ocean populations have. Three mechanisms may have provided such different effects: (1) the sea ice retreat was not even at all longitudes around Antarctica as suggested by de la Mare (1997) and (2) some seal populations fed on prey that were not affected by the environmental changes i.e. prey remained abundant and of high quality and (3) seals in some areas were able to adapt to the changes through shifts in diet perhaps selecting more cosmopolitan prey. However, temporal and spatial information on the diets of elephant seals are still scant for some populations (Burton & van den Hoff 2002) and thus direct comparisons between populations are not possible.

On the other hand, if the decrease in sea-ice and reduced ocean productivity was the cause of the decrease in Indian Ocean and Pacific Ocean elephant seal populations, why have other predators not shown similar patterns of decrease? Antarctic and sub-Antarctic fur seals have been increasing since the 1980s at many sites, as have king penguins. These species were heavily exploited and in most cases the populations were just beginning to re-establish in the 1950s so that their numbers were below a resource impact threshold. However, fur seals and penguins tend to forage locally around their breeding islands (Bonadonna *et al.* 2000; Boyd 1999; Goldsworthy *et al.* 1997; Guinet *et al.* 2001; Moore *et al.* 1999) and hence live in more northern regions less

likely to be affected by sea-ice changes. It seems more probable that fur seal and penguin populations are likely to be affected by lower latitude events such as El Niño (Bonadonna *et al.* 2000; Boyd *et al.* 1994b).

The Southern Hemisphere climate is punctuated irregularly by an El Niño Southern Oscillation (ENSO) event which is the result of changes in the surface winds over the tropical Pacific Ocean (Allan *et al.* 1996). ENSO may affect marine predators in two ways: (1) the affect may be direct, such as affecting the availability of a food source like krill (Murphy & Reid 2001; Priddle *et al.* 1988) or (2) indirectly by affecting sea-ice production (Gloersen 1995) that in turn affects primary production (Smith & Nelson 1985a; Smith & Nelson 1985b). There is a growing body of evidence that has documented such direct effects on a number of marine and land-based predators in the Southern Ocean (Trillmich & Ono 1991; Vergani *et al.* 2001). However, the mechanisms of how physical processes such as ENSO and biological processes are linked remain poorly understood. The results of these studies nonetheless are in accordance with the change in the ocean environment hypothesis.

The indirect effects of ENSO are more difficult to describe, but others have described linkages between ENSO and sea-ice and showed that the effect on sea-ice is strongest in the South Pacific sector of the Southern Ocean (Gloersen 1995). This effect of ENSO also provides some evidence for the differences between the various stocks because the South Pacific region is the region where elephant seals from Macquarie Island are known to forage (Hindell *et al.* 1991a; Hindell *et al.* 1991b; Slip *et al.* 1994). The physical ENSO effects are expressed as variations in sea-ice extent around Antarctica (Gloersen 1995) and are biologically significant because: (1) productivity in the Southern Ocean is allied to sea-ice extent (Knox 1994) and (2) the ecological influence of sea-ice extent has been demonstrated at all trophic levels (Ross *et al.* 1996). Environmental perturbations such as ENSO events may thus affect significantly predator life history traits, such as survival, that rely directly on this productivity.

ENSO intensity and frequency is expected to intensify in the future which would result in greater environmental instability particularly in the South Pacific which in turn would suggest that the populations at Macquarie Island will continue to decrease despite the broader scale stabilization in sea-ice extent. ENSO together with the decrease in sea-ice in the Southern Hemisphere may therefore have resulted in the decreases, and continued decrease, because of the exacerbated effect of two stochastic events acting in unison on the Macquarie population, whilst only sea-ice change acted on the other populations.

Onshore human disturbance

The annual cycle of the southern elephant seal involves two pelagic periods at sea that are punctuated by two periods ashore, one for reproduction and the other for the annual moult (Carrick *et al.* 1962b; Hindell & Burton 1988b; Laws 1956a). It is at these periods ashore that elephant seals are vulnerable to disturbance. Human disturbance may affect a population by: (1) disrupting suckling and the transfer of resources between mother and offspring resulting in lighter pups being weaned (Bryden 1968c) and increased mortality (McMahon *et al.* 2000), (2) males trampling pups during charges at human intruders (Galimberti *et al.* 2000a; LeBoeuf & Briggs 1977) and (3) increasing the occurrence of mother-pup separations (Galimberti *et al.* 2000a; LeBoeuf & Briggs 1977). Until recently, a single survey studying disturbance in elephant seals had been carried out (Wilkinson & Bester 1988). This study found that there was no detectable effect of human disturbance on the elephant seal population at Marion Island as determined by population census information (Wilkinson & Bester 1988). Two recent studies at Macquarie Island (Engelhard *et al.* 2002; Engelhard *et al.* 2001) compared the effects of disturbance on elephant seals at regularly researched beaches with those at sparsely visited beaches. They examined the effect of disturbance by assessing weaning masses and female behavioural responses at the two sites. Weaning mass was selected because it is an easily assessed proxy measurement for maternal investment during lactation (Arnbom *et al.* 1997; Arnbom *et al.* 1993; Fedak *et al.* 1996) and it represents an easily measurable fitness parameter (Arnbom *et al.* 1997; McMahon *et al.* 2000). This study found no differences in weaning masses or behaviours between the beaches with high and low human disturbance (Engelhard *et al.* 2001). Engelhard *et al.* (2002) also quantified the effect of scientific handling chemically by measuring adrenocortical levels in handled and non-handled seals and could not find negative effects associated with handling. Thus onshore human disturbance at current levels does not affect the growth rate of pups or the female's ability to rear and nurse her pup during lactation. Since pup growth and condition at the end of lactation is unaffected by disturbance and mass and condition at weaning is known to influence first year survival (McMahon *et al.* 2000) it seems unlikely that onshore disturbance has any detectable impact on elephant seal population trends. Similarly, others (Kerley 1985; Trites 1991) have found that there was no influence on the growth rates of sub-Antarctic fur seals and northern fur seals (*Callorhinus ursinus*) that had been tagged and handled at birth.

Conclusions

There appears to have been an overall increase in the world population of elephant seals by 11%. Such an increase can be interpreted in three, not necessarily exclusive, ways: (1) that there has

been an increase in the number of elephant seals world wide, (2) that researchers are using more accurate and hence more representative methods for counting seals and (3) that some previously unknown colonies at remote sites have been discovered and incorporated into the present estimate. From the evidence reviewed here the observed increase in southern elephant seal numbers can be best attributed to: (1) actual increases in numbers at some populations such as at Peninsula Valdés and (2) more precise population estimates (McCann 1985) at populations such as South Georgia. Thus, caution is advised when interpreting the reality of this 11.4% increase for conservation/management purposes. It would seem more prudent, on the strength of data from Table 6.1, to conclude that while some populations have clearly increased (Peninsula Valdés) the discovery of new breeding colonies and the difficulties associated with gaining accurate estimates of seal numbers (Boyd *et al.* 1996) may have contributed to the increased estimate of seal numbers and that the world wide population may have been stable since the last review in 1994 (Laws 1994).

It is clear from the literature reviewed here that there is extremely little permanent migration between the four elephant seal stocks. Therefore, monitoring the changes in seal numbers in each population is both possible and important. In addition, if populations are driven to extinction there appears to be no certainty of them being re-colonized through emigration from other more distant sites. The elephant seals once breeding at King Island (Bass Strait) have not returned following their local extinction due to sealing in the 19th century (Bryden *et al.* 1999; Ling 1999). However northern elephant seals (*M. angustirostris*) have colonized islands and beaches in California that were not so distant so that re-colonisation might occur. Counter to this, some populations that are in close proximity to one another have shown little significant migration of females between sites (Hoelzel *et al.* 2001). The present absence of breeding colonies at former breeding grounds such as those on King Island and north-west Tasmania (Bryden *et al.* 1999), where all elephant seals (including females) were hunted to extinction by sealers and hunter-gatherers respectively, provide circumstantial evidence of the effect female philopatry exhibits on the re-colonization of sites. It may be that without a remnant female population nearby, re-establishment of a viable population is unlikely.

Human disturbance during the terrestrial phase of the elephant life cycle has been discounted as a possible contributing factor to the decreases in populations (Engelhard *et al.* 2001; Wilkinson & Bester 1988). This *per se* is not surprising because elephant seals are harem-breeding animals that are exposed to high levels of disturbance from their conspecifics during breeding (Galimberti *et al.* 2000a; LeBoeuf & Briggs 1977; LeBoeuf & Mesnick 1990; McCann 1981; McCann 1982).

Both of the preceding studies (Engelhard *et al.* 2001; Wilkinson & Bester 1988) concluded that human disturbance did not contribute to the decreases in elephant seal numbers, thus further studies assessing the direct effect of human disturbance on survival do not seem to be high priority.

Knowledge of the stock (population) and biomass sizes, and their fluctuations of the elephant seal is vital to our understanding of the Southern Ocean ecosystem. This is because elephant seals comprise a significant proportion of the Southern Ocean biomass (~370 000 tonnes after) (McCann 1985) and hence any attempts to model the energy flow in the overall ecosystem needs to incorporate elephant seals as an integral component of the model. This information, combined with knowledge of the dietary composition and the energy content of their prey allow predictions of annual food consumption by the population (Boyd *et al.* 1994a; Kirkman *et al.* 2000).

Further, examining the energy demands of different age and sex classes can help identify which parts of the population are vulnerable to fluctuations in their food supply or which sections of the population have the greatest impact on resources. Boyd *et al.* (1994a) suggested that despite males contributing nothing to the energetic costs of raising offspring they account for 59% of the energy budget of the South Georgia population. Because males do not contribute to the energetic costs of raising young and because only a few are needed to mate with many females (McCann 1980; McCann *et al.* 1989) they have been largely ignored (Skinner & van Aarde 1983) in assessments of their role in population regulation. Male survival, growth and condition may however be sensitive to environmental change as a consequence of greater (almost twice that of females) energy requirements (Boyd *et al.* 1994a). Consequently, it would seem sensible to include male life history measurements along with those of females in future appraisals of population regulation.

Although it was well known that there were distinct southern elephant seals stocks (Laws 1960) it was not until the advent of molecular studies (Hoelzel *et al.* 1993; Slade *et al.* 1998), foraging ecology studies (Bester & Wilkinson 1994; Campagna *et al.* 1995; Hindell *et al.* 1991a; Jonker & Bester 1998; McConnell *et al.* 1992; McConnell & Fedak 1996; Slip & Burton 1993; Slip *et al.* 1994) and more recently behavioural acoustic studies (Sanvito & Galimberti 2000) that the ecological importance of these sub-populations became apparent. These studies concluded that southern elephant seals were reproductively insular, utilised different areas of the southern ocean for foraging and suggested that different dialects exist between populations that may facilitate reproductive isolation. Accordingly, it has become clear that each of these populations is a

discreet ecological entity and hence, in the search for reasons describing the status of each population it is crucial that each population be treated as a unique case. It may be that rather than there being an overall set of factors controlling all population changes there are different mixes of local and regional factors which do so.

Future research directions

The issue of count accuracy for population estimates is not new but it is very important when it comes to assessing population numbers (Caughley 1977). Elephant seals are difficult to count because they are widespread throughout the Southern Ocean and because, at large island archipelagos such as Îles Kerguelen and South Georgia, seals often haul out at inaccessible locations (Boyd *et al.* 1996). Thus, as a primary objective that underpins future research on elephant seals, multiple, accurate and systematic counts of elephant seals are required at all locations and particularly those locations that support large numbers of seals. This is because changes at such locations, by virtue of their size, will have the biggest impact on the global estimates of southern elephant seals.

By far the greatest gap in the understanding of the foraging ecology of the southern elephant seal is the limited data describing their diets at their distant foraging grounds. Current diet information is restricted to analysis of prey remains directly in lavage samples (Burton & van den Hoff 2002; Daneri *et al.* 2000; Green & Burton 1993; Kastelein *et al.* 1991; Rodhouse *et al.* 1992; Slip 1995). Although these methods have been central to assessing elephant seal diet the results need to be treated cautiously because they mainly provide information on prey species close to haulout sites because elephant seals have highly efficient digestive tracts (Helm 1984; Krockenberger & Bryden 1994). In order to fill this gap it seems likely that other methods are required to augment knowledge of elephant seal diet at distant foraging grounds. For example, methods that integrate diet over long periods such as stable isotope analysis (Burton *et al.* 2001) or fatty acid profiles (Brown *et al.* 1999; Phillips *et al.* 2001; Puppion *et al.* 1992; Rea *et al.* 1997) may prove useful in solving this problem. However, “size of prey” data that are routinely gained from lavaging are not obtainable by biochemical methods. Also sophisticated remote sensing and recording devices may become available in the future that enable the recording of feeding events while the seals are at sea.

In addition to describing the specific diet of elephant seals, describing the *in situ* diets and foraging behaviours of potential resource competitors in a global (Southern Ocean) ecological

context is crucial to the understanding of seal populations. This is because likely competitors such as the larger odontocete whales (*O. orca*, *P. crassidens*, *K. breviceps*, *K. sima* and *P. macrocephalus*), fur seals (*Arctocephalus* spp.) and penguins (*Aptenodytes* spp) that are increasing in numbers may in part be associated with the changes in seal populations (Hindell *et al.* 1994b). Initiation of such projects have previously been suggested (Hindell *et al.* 1994b), however such studies require new techniques and the ability to describe these behaviours concurrently. These tools are not available now but with the advent of ever-smaller electronic storage chips with large memory capacities such multi-species studies may indeed be possible. Furthermore, elephant seals fitted with retrievable/satellite-relayed acoustic or visual monitoring and recording devices may act as platforms (McCafferty *et al.* 1999) from which to measure such interactions.

Understanding how Antarctic predators, such as elephant seals, respond to changes in the distribution of marine resources will be essential to our understanding of the on-going decrease in elephant seal numbers. This is because the oceanic processes that influence the spatial and temporal distribution of primary productivity ultimately determine the demographic performance of apex marine predators like elephant seals. In order to achieve deeper understandings of elephant seal ecology it is necessary to quantify individual and population level responses to large-scale variations in marine resources. Recent satellite imaging techniques now provide tools to measure and track variations in ocean productivity by measuring ocean colour, and thus chlorophyll concentrations, at the sea surface. Together with sea surface temperature, ocean colour can provide a reliable index of the location and magnitude of primary productivity in the Southern Ocean (Arrigo *et al.* 1997; Priddle *et al.* 1998). There are difficulties in gaining temporal data from specific areas due to the very large numbers of clouds in the Southern Ocean (Streten & Troup 1973). Nonetheless, by studying the *in situ* foraging behaviour using established telemetry tools (Guinet *et al.* 2001), reproductive performance and survival of individual seals, links can be established over time that will allow us to quantify the effect of production and demographic performance of elephant seals. In addition to promoting an understanding of present demography of elephant seals, such data will provide knowledge that will lead to new interpretations and predictions of future demographic changes in the light of Antarctic climate change (de la Mare 1997; Stammerjohn & Smith 1997).

The effect on populations and prevalence of southern elephant seal pathogens remain largely unexplored. However, viral pathogens in other seal populations have been implicated in mass mortality events (Kennedy 1998; Kennedy *et al.* 2000; Osterhaus *et al.* 1997; Osterhaus *et al.*

2000; Visser *et al.* 1991) and hence may be important agents to consider when describing the demography of a decreasing population. Although there is no evidence of widespread disease in elephant seals, a recently discovered seal louse arbovirus (SLV) (Linn *et al.* 2001) demonstrates the existence of pathogens in elephant seals. SLV does not appear to be causing any harm to elephant seals for seals that contained antibodies appeared healthy and the presence of neutralising antibodies indicated a successful immune response to SLV. However, alphaviruses have caused many epidemics in birds and mammals, including humans (Strauss & Strauss 1994). The principal pathological dangers, although unmeasured, may be for naïve and/or physiologically stressed individuals. This may be particularly so in species, such as elephant seals that utilise long-range migrations in their foraging activities (Hindell & McMahon 2000). Such long-range migrations, with shared distant haul-out sites, may indeed assist the transfer of disease between populations. Continued searches for viruses in Antarctic seals, and investigations of their pathological effects, may provide new insights for future reviews investigating elephant seal demography. Such investigations need to be widespread and should include both mammals and birds because it is well known that birds are the primary vertebrate host of many viruses and that migratory birds are important agents of dispersal for these viruses (Matrosovich *et al.* 2000; Strauss & Strauss 1994).

Conclusions

1. The demography of two elephant seal populations was examined and compared. This was done to investigate the reasons for the observed decreases in populations at Marion and Macquarie islands. By comparing two decreasing populations I aimed to discover commonalities in the life history traits between islands and thus identify the parameters that may be driving the changes in each of the populations.
2. Hot-iron branding was a swift and reliable method of permanently marking southern elephant seals. A total of 7 000 recently weaned elephant seal pups were hot-iron branded between 1993 and 1999 at Macquarie Island. The branding irons were heated to $\sim 700^{\circ}\text{C}$ in a gas furnace and a mean of $143 (\pm 45)$ seals were marked daily over a period of approximately two weeks each pupping season. First-year survival (corrected for first year brand loss by 2%; and for pre-weaning mortality by 5%) of branded pups was higher (70%) and significantly different from unbranded but tagged pups (62%) from the 1996, 1998 and 2000 cohorts. Wounds that occurred at the time of branding did not affect seal survival ($\chi^2_3 = 0.006$, $p = 0.9$), and the first year survival estimates for these wounded and unwounded pups were similar ($67.34\% \pm 0.017$ and $67.43\% \pm 0.013$ respectively). The heart rates of five pups were measured one minute prior to branding, during restraint, during branding, and two minutes and 10 minutes after branding. There was a significant elevation in heart rate following restraint, followed by a significant decline ($t_4 = 3.9$, $p = 0.018$) during branding (while the brand was applied). Heart rate returned to resting levels 10 minutes after branding. Cryo-branding was trialled but did not yield visible brand-marks in the years following. In conclusion, hot-iron branding is a rapid and reliable method of permanently identifying elephant seals, avoids some of the disadvantages of conventional tagging, does not prejudice survival and does not appear to cause undue stress to individuals.
3. To quantify the effect of marking and handling pups, 500 pups were repeatedly handled during the first six weeks of life at Macquarie Island and the effect of this handling on first year survival was measured. Repeatedly handled individuals, subject to potentially invasive research methods, had no measurable difference in survivorship between handled and not handled seals and hence fitness one year after handling. This is believed to be in part due to the harem environment in which young elephant seals live. Life in the harem is disruptive and hazardous to the young pups. Thus the species as a whole may be pre-adapted to disturbance.

Because repeated handling, for research purposes, during the first weeks of life did not influence survival it was very unlikely to have had an effect on the population size of southern elephant seals at Macquarie Island.

4. In order to estimate concurrent age specific survival for southern elephant seals at Macquarie and Marion islands, seals were marked from 1993 to 1997 in the first three weeks of life and resighted (recaptured) on return to their natal islands (1993-2001). These recaptures formed the basis for the survival analysis in the mark-recapture program MARK. Weaning masses were also collected at each location and used to estimate the effect of weaning mass on post weaning survival in the first year of life. Recapture probabilities were significantly ($\chi^2_6 = 376.480, p < 0.0001$) higher at Marion Island than at Macquarie Island. There are two possible reasons: (1) the population at Marion Island is smaller and less dense than at Macquarie Island and (2) seals hauled out along a smaller section of the coast at Marion Island than at Macquarie Island, which: (1) facilitates the detection and individual identification of seals and (2) increases access to hauled out seals. Age specific survival estimates differed ($\chi^2_5 = 22.264, p < 0.05$) at the two islands and were consistently higher at Macquarie Island. The survival estimates for male and female seals were different at both Macquarie Island ($\chi^2_6 = 34.657, p < 0.0001$) and Marion Island ($\chi^2_6 = 20.373, p = 0.002$). Female survival estimates were consistently higher than male survival estimates. The combined survival estimates for juvenile seals (1-3 years) differed between islands and survival of older seals (4-6 years) did not. The inclusion of gender in the survival models did not improve model performance and hence male and female estimates were considered jointly to test the effects of weaning mass on first year survival. The mean wean masses of male and female seals combined from 1993-1998 were not significantly different between islands ($T_{6837} = 1.169, p = 0.242$). At Macquarie Island the mean wean mass was 118.8 kg (SD = 27.2, n = 6504) while at Marion Island the mean wean mass was 120.6 kg (SD = 24.7, n = 335). Wean mass influenced survival differently at the two island locations ($\chi^2_{16} = 38.664, p = 0.0012$). At Macquarie Island wean mass influenced first and second year survival, but only first year survival at Marion Island. The mean age at first breeding was different ($p < 0.001$) in the two island populations. At Macquarie Island the mean age of first breeding was 4.68 years \pm 0.38, and at Marion Island it was 3.95 years \pm 1.03. More ($\chi^2_1 = 67.39, p < 0.0001$) three-year-old females breed at Marion Island (28.7%) than at Macquarie Island (1.2%) and the proportion of seals that had bred at least once by age seven was greater

at Marion Island than at Macquarie Island. I concluded that the observed decreases in elephant seal numbers between the 1950s and 1990s in the Pacific and Indian Ocean sectors were driven by resource limitation in the Southern Ocean. A conglomerate of factors including local predation by killer whales and intra-specific resource competition is postulated as a cause for the inter-island (regional) differences in population trends. Presently it appears that *per capita* more resources are available to the Marion Island population than are available to the Macquarie Island population.

5. Population trajectories were simulated for three populations of southern elephant seal. These populations, at Marion Island and Macquarie Island, are decreasing, albeit at different rates, while the South Georgia population is stable or increasing. The population projections that were simulated from life-history tables accurately described the independently derived (from annual abundance surveys) population trends observed at Marion Island (1986-2001) and Macquarie Island (1986-2001). The standard deviations (SD) of the estimated vital rates were used in the simulations as a measure/proxy for environmental variability and determined that small changes in the environment that affect survival and fecundity may have a dramatic outcome on population growth rates. At Macquarie Island a small change (*circa* 5%) in the environment, that increases maximal survival and fecundity rates, results in the population changing from a decreasing mode to an increasing one. While such small changes may have notable effects on the Macquarie Island population, this was not true for Marion Island where the population continued to decrease even with the same changes in the environmental factor. Interpretations from the simulations run on the South Georgia population were problematic as estimates of vital rates there were not accompanied by estimates of variability. Thus mean estimates of variability from the Marion and Macquarie Island populations were used in the simulation. The inability to calculate estimates of variability from cross-sectional studies highlights their limitations. The vital rates that had the greatest impact (elasticity) on fitness (population growth) for all populations i.e. Marion Island, Macquarie Island and South Georgia, were, in order of importance: (1) juvenile survival, (2) adult survival, (3) adult fecundity and (4) juvenile fecundity. At Marion Island juvenile and adult survival contributed equally to the fitness of the population while at Macquarie Island and at South Georgia Island juvenile survival was more important than adult survival in determining population fitness. Population viability analysis (PVA) for each of the two decreasing populations revealed that there was a high probability of the Marion Island population becoming extinct within the next 150 years $p = 1.00$ while the probability of extinction at Macquarie Island was low $p = 0.00$.

The estimated times to extinction was 134 years (105-332 years) at Marion Island and at Macquarie Island time to extinction was 564 years. The earliest time to extinction at Macquarie Island was 307 years.

6. The global population of elephant seals in 2001 was estimated at approximately 738 772 which represents an increase of 11.4% from the last world estimate (664 000). Four main stock populations are recognized namely: (1) South Georgia, (2) Peninsula Valdés, (3) Kerguelen and (4) Macquarie Island. While some breeding populations have continued to decrease in recent years (Macquarie Island and Marion Island) (Bester & Wilkinson 1994; Hindell *et al.* 1991a; Hindell *et al.* 1991b; LeBoeuf *et al.* 2000; Slip *et al.* 1994) others have either remained stable (South Georgia, Îles Kerguelen and Heard Island) or increased (Peninsula Valdés). The reasons for these differences in population behaviour remain unknown, although it would appear that predation of naïve pups when first entering the water may be an important factor in keeping small populations, such as Marion Island, small. Prey (food) availability has been identified as the primary factor determining life history traits such as growth, primiparity and survival and regional differences in primary productivity within the Southern Ocean may account for many of the differences in population demographic behaviour.
7. In recent years research has been conducted to assess the impact human activities (research and commercial, e.g. fishing) may be having on the elephant seal populations. It seems clear from the evidence presented and reviewed here that the present changes in seal populations, unlike the period of direct exploitation in the 19th and 20th centuries, are neither a consequence of direct human interactions nor present-day commercial activities. While the significance of inter-specific competition between elephant seals and other Antarctic predators remain largely unknown or quantified, it would seem prudent that these relationships be studied. This is because many of the potential resource competitors (toothed whales) have been increasing in number since the cessation of commercial whaling. Although in principle easy to describe, quantifying these relationships is problematic because the *in situ* (foraging zone) diet of elephant seals is poorly known and the diet and foraging areas of the toothed whales remain almost completely unknown. Confounding the paucity of dietary overlap information, there is also almost no data describing the spatial and temporal overlap at sea of elephant seals and toothed whales. Through researching and understanding the food web structure and inter-relations between these Antarctic predators, some more insights into

the nature of the decreases in elephant seal populations may be identified. Such studies may also facilitate the management of the Southern Ocean ecosystem for CCAMLR purposes.

Summary

This study addressed and determined the possible cause/s that might be driving the decreases in southern elephant seal populations at Marion Island and at Macquarie Island. Two decreasing populations, one small (Marion Island) and one relatively large (Macquarie Island), were chosen for the comparison so that demographic similarities could be discovered. This was because demographic parameters that were common to both populations and indeed a third population at South Georgia (published data only) were judged as those having the greatest impact on population growth.

At Marion Island seals were marked with flipper tags and at Macquarie Island they were marked with hot iron brands. Thus, two populations of known-aged individuals were available for life history studies. The efficacy of tagging has been determined previously and found to be reliable although some difficulties such as tag loss have been identified. The efficacy and reliability of hot branding had not been previously rigorously tested. I determined that hot branding was an efficient and reliable way to mark seals up to age eight, and from previously published information it is known that brands will remain for the entire life of an elephant seal. The study of population demographics may be considered invasive because animals are repeatedly handled. The effect of handling was quantified in terms of survival and it was found that handling during the first weeks of life did not affect survival in the first year. Thus having determined that the marking system was effective and that handling and marking seals did not compromise survival it was possible to compare the life history of the seals at the two islands.

At Macquarie Island survival was higher and age at first breeding was earlier at Marion Island, and there was a significant increase in the mean wean mass of seals at Marion Island but not at Macquarie Island. These observations of earlier primiparity and increased wean mass at Marion Island suggested that more resources were available to the seals at Marion Island in comparison to those at Macquarie Island but could not explain why if there was more food why survival was lower. One possible reason for this was that predation by killer whales was higher at Marion Island than at Macquarie Island, and that the effect of this predation would be more pronounced in a small population (Marion Island) relative to a large one (Macquarie Island). To determine which of the life history parameters are most important in terms of population change I designed a stochastic population model that had as inputs the observed rates of survival and fecundity at each island. This allowed me to project the size of each island population and compare these to those observed in the field. An elasticity analysis was used to determine those stages (or ages)

that were most crucial to population change. The model was a good representation of the empirically determined data and overall juvenile survival was most important in determining population change although at Marion Island both juvenile and adult survival were almost equally important. Furthermore, neither the Marion Island nor the Macquarie Island populations were in immediate (100 years) danger of extinction. Indeed there is a 30% chance that the Macquarie Island population could increase if all the demographic parameters remained constant.

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