LIFE HISTORY PARAMETERS AND REGULATION OF THE SOUTHERN ELEPHANT SEAL POPULATION AT MARION ISLAND

by

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SUMMARY

Pup mortality of southern elephant seals at Marion Island from 1990 through 1999 ranged from 1.6 to 7.3%, averaging 3.8%. Pup mortality was density independent and dismissed as being a major population regulating agent at Marion Island.

Juvenile survival over two periods, one during the population decline and the other after the population had stabilised, was assessed and compared using mark-recapture models. Survival was age- but not sex-related and on average, the probability of survival was 59.5%, 81.4% and 78.1% for the first, second and third year respectively. There was no significant difference in survival over the two periods and juvenile survival does not appear to be an important population regulating component in the southern elephant seal population.

Mark-recapture data for females from the Marion Island population since the population stabilisation (1994) was analysed and compared with similar data collected during the decline and with data collected from the increasing population in southern Argentina. Survival of prime-age adult females increased by 8% concurrent with the stabilisation at Marion Island, which ultimately compensated for an annual rate of decline of the population of 5.85% until 1994. Survival of adult females at the colony in southern Argentina was 6% greater than at Marion Island after the stabilisation. Adult female survival is concluded to predominantly regulate the population.

Changes in adult female survival and breeding probabilities with age were quantified in order to measure the prevalence of senescence in the population. Less than a 1% difference between prime-age and post prime-age survival was found over eight cohorts of marked females and no evidence of reproductive senescence in terms of reduced breeding probability with age was detected. Five percent of southern elephant seal females survived to age ten and 0.5 % to the age of seventeen.

Pubescent male survival increased concordant with the population stabilisation. These animals have high energetic demands due to a secondary growth spurt during which growth is accelerated and this increase lends support to the hypothesis that food has been limiting the population at Marion Island.

Future survival and breeding probabilities of females primiparous at different ages were estimated in order to investigate potential future fitness costs associated with early breeding. Annual future survival of females breeding at age three was the same as that for females primiparous at four and slightly higher than that for females primiparous at five and six. Future breeding probabilities of females primiparous at three were similar to that for females primiparous at four and older. I found no evidence for future fitness costs incurred through reproductive expenditure and conclude that age of primiparity is determined by acquisition of a critical body mass, after which no future delay in reproduction takes place.

I estimated future survival and capture probabilities of southern elephant seals that winter at Marion Island during their first three years and compared these values to similar estimates from individuals that were not observed to winter over the same time periods. There were no significant differences in survival between wintering and non-wintering elephant seals suggesting that survival is not a fitness correlate of wintering behaviour. I provide unique evidence of differential site fidelity within age- and sex classes, which has implications for population modelling.

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CHAPTER 1 GENERAL INTRODUCTION

1.1 Introduction

Proximate factors responsible for changes in population growth rate form a central theme in population ecology and bear practical as well as theoretical importance (Gaillard *et al.* 1998). Longitudinal studies of populations with various growth rates are particularly useful for the purpose of elucidating such factors.

Numerous studies have quantified the vital rates pertaining to specific populations at a given time and this has greatly enhanced our understanding of population dynamics. To determine what influence the respective population parameters have on population growth (i.e. which parameters are responsible for regulating the population) and the identification of limiting factors is the ultimate goal to allow for sound population management and for predictive purposes. This requires the comparison of vital rates between populations with varying growth rates so as to quantify the changes in these vital rates that bring about population change. Long-term studies of populations with varying growth rates can be used to identify which vital rates are the most important in influencing population growth and thereby regulating populations (Toigo *et al.* 1997).

Elephant seals are particularly immobile on land compared with most other large mammals. Their haulout patterns are also highly predictable. These features greatly facilitates the ease with which they are marked and recaptured (physically or by visual inspection) and makes them ideal subjects for long-term demographic studies.

The demographics of southern elephant seals have received ample attention in recent years partly as a result of the observed declines in several of these populations, particularly those in the southern Indian and Pacific Oceans (Condy 1978; Bester 1980; Skinner & Van Aarde 1983; Pascal 1985; Burton 1986; Hindell & Burton 1987; Guinet *et al.* 1992; Bester & Wilkinson 1994). At least some of these populations now appear to have stabilised (Guinet *et al.* 1999; present study), while the Atlantic Ocean populations have been stable or increasing (Laws 1994), with the exception of the small Gough Island population which has shown a long-term decline (Bester *et al.* 2001). The Marion Island population declined about 37% between 1986 and 1994 (5.8% annual rate of decline) from 2120 to 1330 seals (Pistorius *et al.* 1999b), and has been stable since 1994 (Chapter 5). These two periods will subsequently be referred to as the declining and stable phase respectively and will form the basis for comparative studies within this thesis. At several stages in this thesis I attempt to generalise my results to other elephant seal populations. It is important to note that the Marion Island population is a very small population relative to other populations (see below) and may be subject to different environmental circumstances thereby reducing the confidence placed on such generalisations.

1.2 Biology of the Southern Elephant Seal

The southern elephant seal is the largest in size of the 34 extant species of pinnipeds (King 1983). It is one of the most sexually dimorphic marine mammals, with sexual dimorphism becoming apparent after the age of one is reached (Bell *et al.* 1997), and is extremely polygynous by comparison with any other large vertebrate (Le Boeuf & Laws 1994). A fully grown adult male has been recorded to weigh up to 3700 kg (Ling & Bryden 1981), compared to 400-600 kg for females (Fedak *et al.* 1994). Although puberty in southern elephant seal males is reached between about four and six years of age (Laws 1956a & b; Carrick *et al.* 1962a), social maturity is only attained at about eight years of age (Laws 1984). All females are recruited into the adult population at age six (Wilkinson 1992). A longevity of 20 and 23 years have been recorded for males and females respectively (McCann 1985; Hindell & Little 1988), although animals very seldom reach these ages (present study).

Laws (1977) suggested that the diet of elephant seals consists of 75% squid and 25% fish by weight, but this proportion has been contested (Slip 1995). Estimates of diet based on the hard remains of prey are likely to overestimate the importance of squid due to the presence of a hard beak, since elephant seals have a fast gut passage rate, and anything eaten more than four hours before they return to land is likely to be completely digested (Hindell *et al.* 1991). More reliable information is scarce due to the obvious difficulties in collecting such data. Depending on the locality, there appears to be differences in the diets of at least some of the elephant seal populations (Green & Burton 1993).

Elephant seal males and females spend approximately eight months and 10 months a year at sea respectively, and the rest of the time on land during two distinct and highly predictable terrestrial phases (Carrick *et al.* 1962b; Condy 1979; Hindell & Burton 1988;

Wilkinson 1992; Laws 1994) namely the breeding and moulting phases. Immature individuals also have a short winter haulout period to which no specific function has as yet been ascribed (Condy 1979).

1.2.1 Terrestrial phases

The breeding season for southern elephant seals at Marion Island commences in mid-August when the adult males start hauling out and competing for dominance on beaches. They are joined by the first pregnant females in the beginning of September, that gradually congregate in harems and reach a maximum number on the 15th of October (Condy 1979; Wilkinson 1992). Cows give birth approximately one week after they have hauled out. The post-partum period before the pup is weaned lasts between 19 to 25 days, and the female leaves the harem soon after (Wilkinson 1992). Mating takes place approximately 18 days after parturition and the dominant males obtain over 98% of the matings (Wilkinson 1992). Assistant beachmasters are not often encountered on Marion Island due to the relatively small harems (Wilkinson 1992). The mature, subordinate males remain around the edge of the harems. The males return to sea in mid-November after having fasted since the beginning of the breeding season. The non-breeding females are rarely seen on land during the breeding season and those mating for the first time probably do so at sea during this period (Laws 1956a).

Moulting is the second annual event that ties elephant seals to land and entails the shedding of skin and hair in great patches. Elephant seals haul out on land during a certain time, depending on sex and age, and remain there until the moulting process is completed. Yearlings moult between mid-November and the end of January, adult females, after feeding at sea following the breeding season, moult between mid-December and mid-March, and adult males moult between mid-December and mid-April (Condy 1978). Sub-adults moult between beginning November and March (Condy 1978). Elephant seals fast during both terrestrial phases.

1.2.2 Pelagic phases

A substantial amount of research on elephant seals has in recent years been aimed at elucidating the foraging migrations of elephant seals (Bester 1989; Boyd & Arnbom 1991; Hindell *et al.* 1991; Bester & Pansegrouw 1992; McConnell *et al.* 1992; Slip *et al.* 1994; Stewart & De Long 1994; Campagna *et al.* 1995; McConnell & Fedak 1996; Jonker & Bester 1998). This has shown that despite fidelity to their natal islands, elephant seals range widely in the southern hemisphere, often visiting the continents abutting on the Southern Ocean, and range as far south as the pack-ice region and the Antarctic continent (Bester 1989). They make biannual, round trip migrations lasting two to eight months and covering 2000-7500 km, during which they dive continuously (Campagna *et al.* 1995). Postbreeding and postmoulting females from Marion Island appear to range up to 1460 km and 3133 km respectively (Bester & Pansegrouw 1992; Jonker & Bester 1998). Adult females from Marion Island appear to concentrate their feeding largely within inter-frontal zones south of the Antarctic Polar Front and between the Sub-Tropical Convergence and the Sub-Antarctic Front at oceanic frontal systems, with postmoulting females foraging further afield up to the pack ice (Jonker & Bester 1998). Adult males, on the other hand, stay relatively close to Marion Island pursuing pelagic prey species in very deep water (Malherbe 1998). Southern elephant seals have been shown to travel for prolonged periods at speeds of around 70-80 km/day, and in total, their foraging distribution could cover three-quarters of the Southern Ocean (McConnell & Fedak

1996). Dives of up to 1452 and 1444 meters have been recorded for adult males and females from Marion Island respectively, and dives can last up to 113 minutes (Jonker & Bester 1994; Malherbe 1998).

1.3 Distribution & Present Status of Southern Elephant Seal Populations

Southern elephant seals have a circumpolar distribution in the Southern Ocean (Fig. 1) with major breeding populations occurring close to the Antarctic Polar Front (Laws 1994). Laws (1960) proposed that the world population of southern elephant seals can be divided into three almost totally independent sub-populations namely the Kerguelen stock, the South Georgia stock and the Macquarie stock. The Kerguelen stock comprises Iles Kerguelen and Heard Island, Marion and Prince Edward islands, and Iles Crozets; the South Georgia stock consists of South Georgia, King George Island, South Orkney Islands, South Shetland Islands, South Sandwich Islands, Gough and Bouvet islands, together with South America and the Falkland Islands; and finally the Macquarie stock includes Macquarie Island, Campbell Island, Auckland Islands, and Antipodes Islands. Recent genetic studies suggested that the Falkland Islands and the South American group are, however, separate from the South Georgia stock and therefore may constitute a fourth elephant seal stock (Slade 1997). The total world population of southern elephant seals was estimated at 664 000 in 1990, of which South Georgia and Peninsula Valdés accounted for 60%, Iles Kerguelen 28%, and Macquarie Island 12% (Laws 1994).

Of the South Georgia stock, the population at South Georgia itself appears to have been stable since 1951 (Laws 1960; McCann & Rothery 1988; Laws 1994; Boyd *et al.* 1996), while the King George Island and Gough Island populations have been declining at 5.7% and 3.3% respectively (Vergani & Stanganelli 1990; Bester *et al.* 2001). The Peninsula Valdés population has been increasing at between 3.6% and 5.1% annually since 1975 (Vergani *et al.* 1987; Lewis *et al.* 1998). Both the Iles Kerguelen and Macquarie Island stocks have declined steadily over the last forty years (Van Aarde 1980; Hindell & Burton 1987; Guinet *et al.* 1992), although the Iles Kerguelen and Crozet populations seem to have recently stabilised (Guinet *et al.* 1994; Guinet *et al.* 1999) and the Heard Island population now appears to be increasing (Slip & Burton 1999). The Marion Island population declined by almost 90% between 1951 and 1994 and in percentage terms has been the most adversely affected of all except those at Signy Island and Campbell Island (Condy 1978; Bester & Wilkinson 1994; Laws 1994; Pistorius 1999b). This population has been stable since 1994 at about 1700 individuals, including pups (Pistorius *et al.* 1999b; present study).

Figure 1. Breeding distribution of southern elephant seals in 1990. Circles indicate known breeding colonies and areas of circles are proportional to the estimated population sizes except for colonies of less than 5000 (Modified from Laws 1994).

1.4 Objectives of the Study

The aim of this study is to compare vital rates within the Marion Island population during the phase that the population was declining with similar rates after the population has stabilised as well as with vital rates from the increasing population in Patagonia, South America. This is done in order to identify the population parameters that have been influential in driving the population decline and to quantify the changes in these rates that have resulted in the observed changes in the population growth rate. The ultimate aim is to attempt to identify which vital rates regulate the southern elephant seal population at Marion Island and to determine what limits the population. Other life history aspects of the population, including fitness costs of age of primiparity and the prevalence of senescence in the population are also investigated.

I start off exploring pup mortality before the first pelagic phase in the population and test for density-dependence in pup mortality, as this is a prerequisite for population regulation (Chapter 3). I also identify agents of mortality in pups and contrast them over various sized harems.

In Chapter 4 I aim to estimate post-weaning juvenile survival over the first three years of life for the period that the population was stable (1994-1999). I contrast these survival estimates with similar estimates during the population decline to determine whether this population component has been influential in regulating the population. I also test for age-, sex- and time dependence in juvenile survival using recently developed mark-recapture methodology.

The aim of Chapter 5 is to estimate adult female survival during the period that the Marion Island population was stable, and to compare this to similar estimates while the population was declining. Adult female survival in the increasing population at Peninsula Valdés (Patagonia) is also estimated from longitudinal mark-recapture data and compared to estimates from Marion Island.

In Chapter 6 I aim to investigate the prevalence of senescence in the elephant seal population in terms of reduced survival and breeding probabilities with age. To my knowledge this is the first longitudinal study of senescence in pinnipeds.

In Chapter 7 I estimate pubescent male survival during and after the population decline and test for a density dependent increase in survival concurrent with the population stabilisation. This population component is characterised by exceptionally high energetic requirements invoked by the secondary growth spurt. If food availability has been the ultimate cause for the decline and hence the limiting factor, I expect an increase in survival of these animals as the population stabilised.

In Chapter 8 I assess life history consequences of early primiparity in southern elephant seal females in terms of future survival and reproduction. This is done to determine whether future reproductive costs are incurred through reproductive expenditure as predicted by life history theory.

In Chapter 9 I aim to determine if there are any fitness connotations associated with wintering behaviour in juvenile southern elephant seals.

Predation is often responsible for regulating populations (Caughley & Sinclair 1994). Killer whales are the only predators of elephant seals at Marion Island. I include a study based on limited data of killer whale abundance and the potential impact it may have on the elephant seal population (Appendix 1).

The content of this thesis consists of several papers that are structured for scientific journals and I apologise for overlap in the description of methods used between the chapters.

CHAPTER 2 STUDY AREA

2.1 Location

Marion Island (46°54′S, 37°45′E) is located in the southern Indian Ocean, approximately 2180 km south-east of Cape Town, and about 1770 km south south-east of Port Elizabeth, South Africa. It is situated about 2300 km north of Lutzow-Holm Bay, Antarctica (Fig.1). Marion Island and Prince Edward Island together form the Prince Edward Islands. The closest land mass to these islands is Ile aux Cochons of the Crozet Island Group, a French possession, about 950 km to the east.

2.2 General Description

Marion Island is about 290 km^2 in extent with an oval-shaped coast-line of approximately 90 km (Fig.2). It measures 24 km from east to west and 17 km from north to south. Close to 138 km^2 of Marion Island are below 200 m altitude and the highest peak is 1230 m above sea level (State President Swart Peak). The island has a low dome-like profile, broken by several conical hills comprised of volcanic ash and scoriae and consists of three distinct

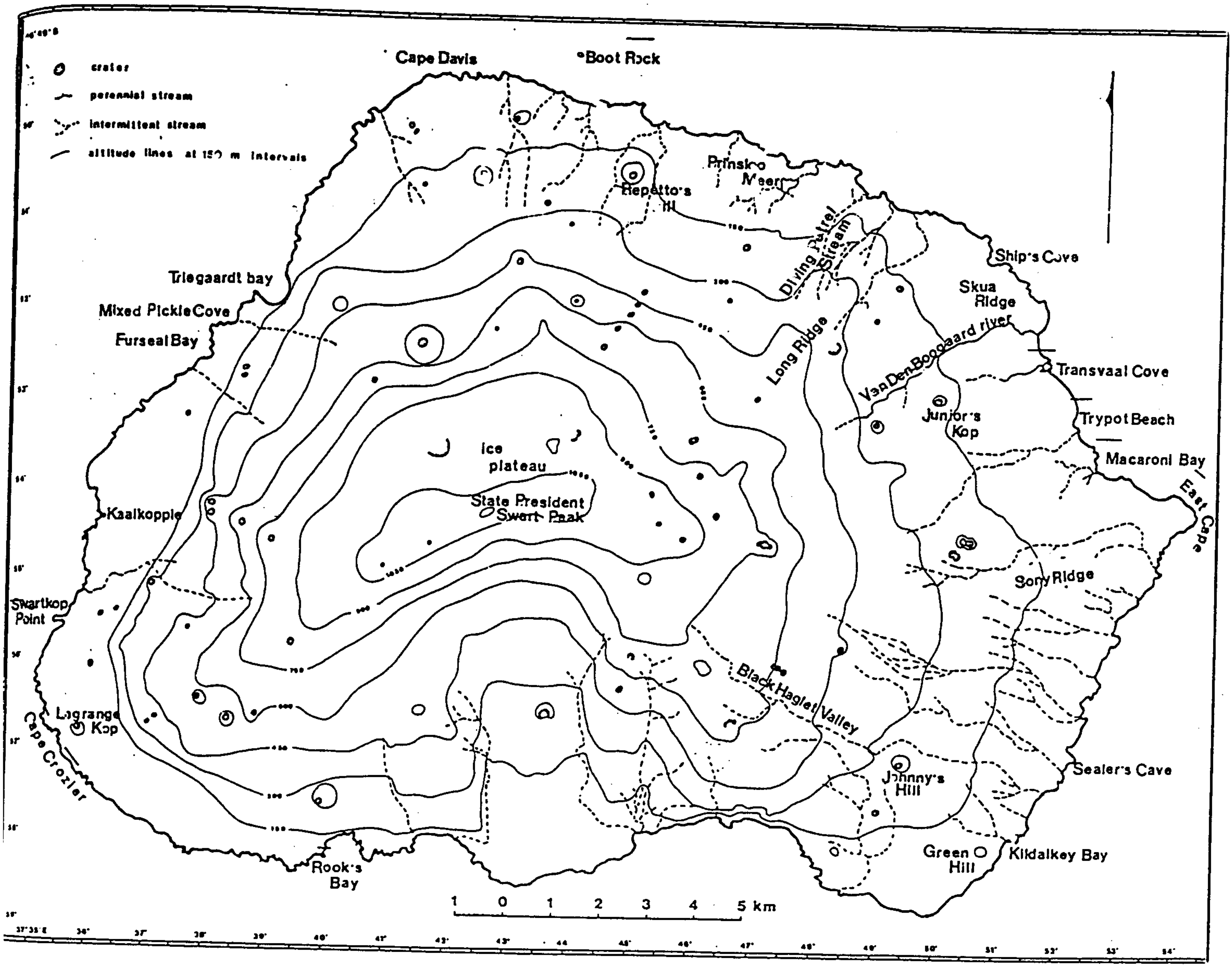

Figure 2. Topographical map of Marion Island (taken from Gremmen 1981).

physiographic regions. These include a central highland and an island slope separated by an escarpment from a coastal plain in the south-west.

The central highland is a plateau surmounted by a series of volcanic cones responsible for the serrated skyline of the summit area. The island slope comprises the majority of the island surface and extends from the central highland down to the north, east and south-east coasts and the edge of the escarpment in the west. The coastal plain which lies at the foot of the western escarpment is a volcanic outbuilding rather than a raised marine terrace. The coastline on the western side of the island is irregular, and generally terminates in vertical cliffs up to 15 m high. The eastern coastline is flatter and more regular in appearance, allowing easy access for elephant seals.

2.3 Climate

Systematic meteorological observations made at Marion Island are available since 1948, and it is evident that the climate is pre-eminently marine except insofar as it is modified by the topography of the island itself. The climatological conditions on Marion Island are brought about by the interchange of sub-tropical and subantarctic air through the agency of numerous depressions or extra-tropical cyclones.

The outstanding climatic features are:

1. Predominantly strong westerly winds, often of gale force.
2. High relative humidity, with little annual or diurnal variation from 80%.
3. Relatively low mean temperature (about 5°C) showing little annual or diurnal variation, with only about 29% sunshine per year. Temperatures as low as -4°C to -6°C occur frequently throughout the year.

4. Abundant precipitation in the form of rain, snow or graupel (ice-rain) with a mean annual precipitation of ± 2500 mm, spread fairly evenly throughout the year.
5. A high degree of cloud cover, with only 20-33% of the possible amount of sunshine reaching the island surface.

A feature of importance in this oceanic region is the Antarctic Polar Front, which is the boundary between cold, poorly saline Antarctic surface water and less dense warmer subantarctic water.

CHAPTER 3 PUP MORTALITY IN SOUTHERN ELEPHANT SEALS AT MARION ISLAND

3.1 Introduction

At Marion Island, pregnant southern elephant seals haul out from early September through October, with peak numbers ashore around 15 October (Condy 1979). Pups are born about a week after females haul out and are then nursed for about 19-25 days before being weaned abruptly when their mothers go back to forage for about two months (Condy 1979; Wilkinson 1992). Once weaned, pups remain ashore continuously for 6 to 10 days, before they begin to explore the near-shore marine environment for several hours or more, usually between dusk and dawn (Lenglart & Bester 1982). When about two months old, pups depart the colony and remain at sea foraging for several months (Condy 1979; Wilkinson & Bester 1990).

Though pup survival during the first year has been partially described (Pistorius *et al.* 1999a), it has as yet not been described for pups through weaning or just after weaning before they go to sea. This pre- and post-weaning mortality of pups ashore may be an important dynamic component accounting for variability in recruitment and population trends, especially for the population at Marion Island where births declined substantially from the 1950s through at least 1993 (Bester & Wilkinson 1994; Pistorius *et al.* 1999a,b). Here we describe patterns of survival of pups from birth to weaning and during the several weeks after weaning before pups go to sea. If pre-weaning mortality is adversely affected by density of breeding animals ashore, as suggested by some authors (i.e. Le Boeuf & Briggs 1977), then we expected pup survival to have increased in recent years as a compensatory response in a declining population.

3.2 Methods

We counted all seals ashore at each beach at Marion Island each week between August and November each year from 1990 through 1999. We recorded live and dead pups, and numbers of adult females during each survey. To prevent recounting, we either clearly marked or removed dead pups from all beaches during each survey. We calculated total percentage pup mortality for every year as the proportion of those born that died prior to weaning (pre-weaning mortality) or just after weaning but before departing to sea (post-weaning mortality; cf. Wilkinson 1992; Pistorius *et al.* 1999a,b). The weaning status of dead pups was determined through visual assessment of the pelage and distance of the dead pup from the harem. We did a correlation of number of pups born in each year (linearly diminishing numbers over the study period (see Pistorius *et al.* 1999a)) and annual pup mortality for the period 1986 to 1999 to determine whether mortality was related to the number, and perhaps density, of seals at breeding sites. Pup mortality and births for 1986 through 1989 were taken from Wilkinson (1992). We also regressed pre-weaning mortality on the number of females m^{-2} of beach (an index of density) at peak season (i.e., 15 October – Wilkinson 1992) at 12 sites. In addition, we regressed average pup mortality against average harem size (grouped into intervals of five) over the study period.

We examined the influence of the age composition of marked breeding females (see Pistorius *et al.* 1999a for details on the mark-recapture program) at the various sized harems on patterns of pup mortality in an attempt to explain discrepancies in pup mortality in different sized harems. Ages of females were determined from uniquely-numbered tags that had been placed in their hind flippers at birth (see Pistorius *et al.* 2000). We predicted that younger female age distributions may be evident in smaller harems and that inexperience in motherhood may have caused the higher pup mortality in small harems.

3.3 Results

Overall, annual pup mortality was low, averaging 3.8%, and ranged from 1.6% to 7.3% (Table 1). Virtually all mortality occurred before pups were weaned. Indeed, only one to four ($\bar{x} = 2$) pups died on the island each year after they were weaned but still ashore. Pup mortality was independent of births and female abundance at peak season (as an index of density; $r^2 = 0.0187$, $p = 0.165$; $r = 0.456$, $p > 0.05$). An inverse exponential relationship was found between pup mortality and harem size (Fig. 1). Smaller harems had a significantly larger proportion of inexperienced (three- and four-year old) females than larger harems (Fig. 2).

Table 1. Pup mortality in southern elephant seals at Marion Island (pw = pre-weaned, w = weaned).

Year	*1990*	*1991*	*1992*	*1993*	*1994*	*1995*	*1996*	*1997*	*1998*	*1999*	***Average***
Dead pups (pw)	17	12	12	11	18	31	13	9	26	4	15.3
Dead pups (w)	1	4	1	3	3	2	1	1	1	3	2
Births	502	492	473	478	423	451	428	421	430	431	453
Pup mortality	3.59%	3.25%	2.75%	2.93%	4.96%	7.32%	3.27%	2.38%	6.28%	1.62%	3.8%

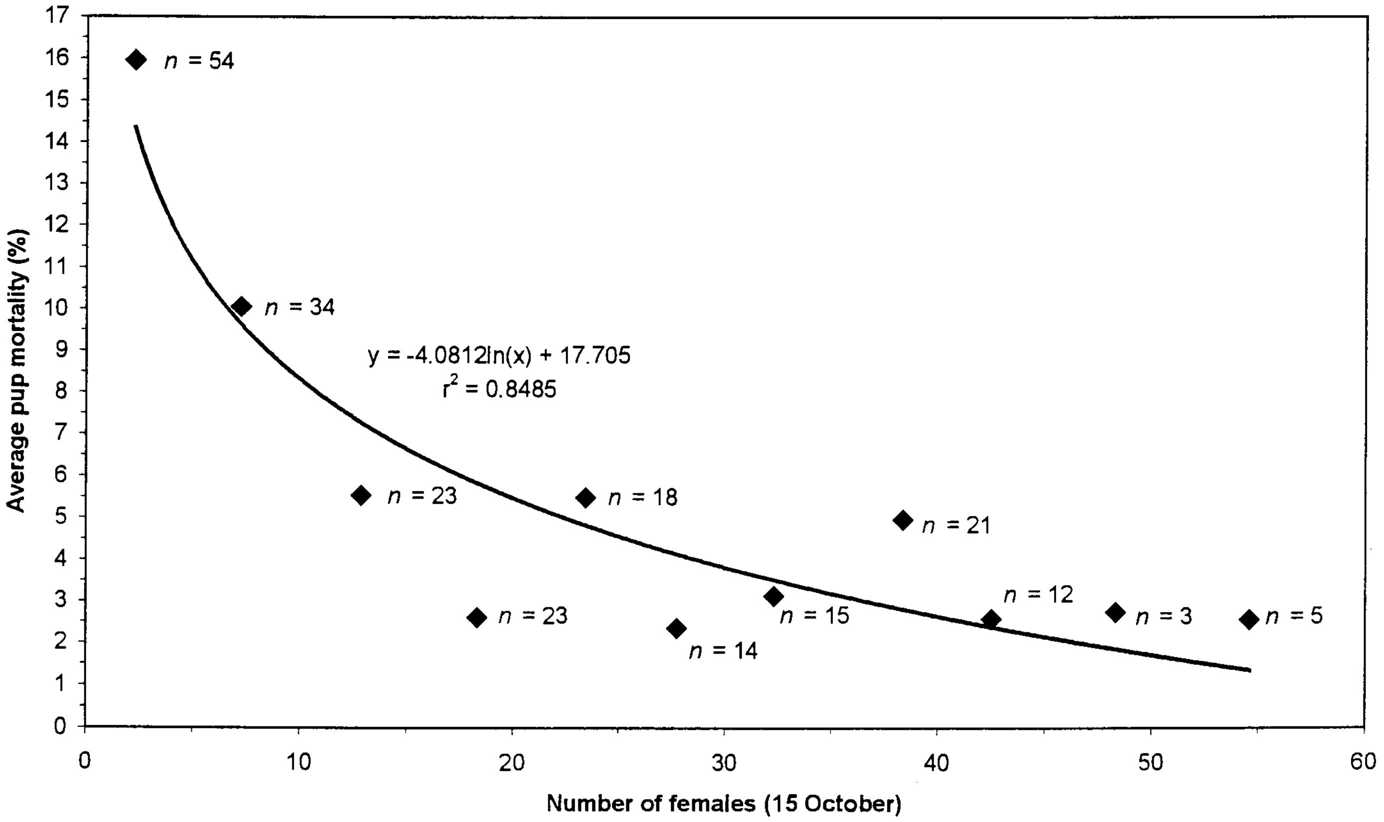

Figure 3. Pre-weaning pup mortality in different sized harems at Marion Island.

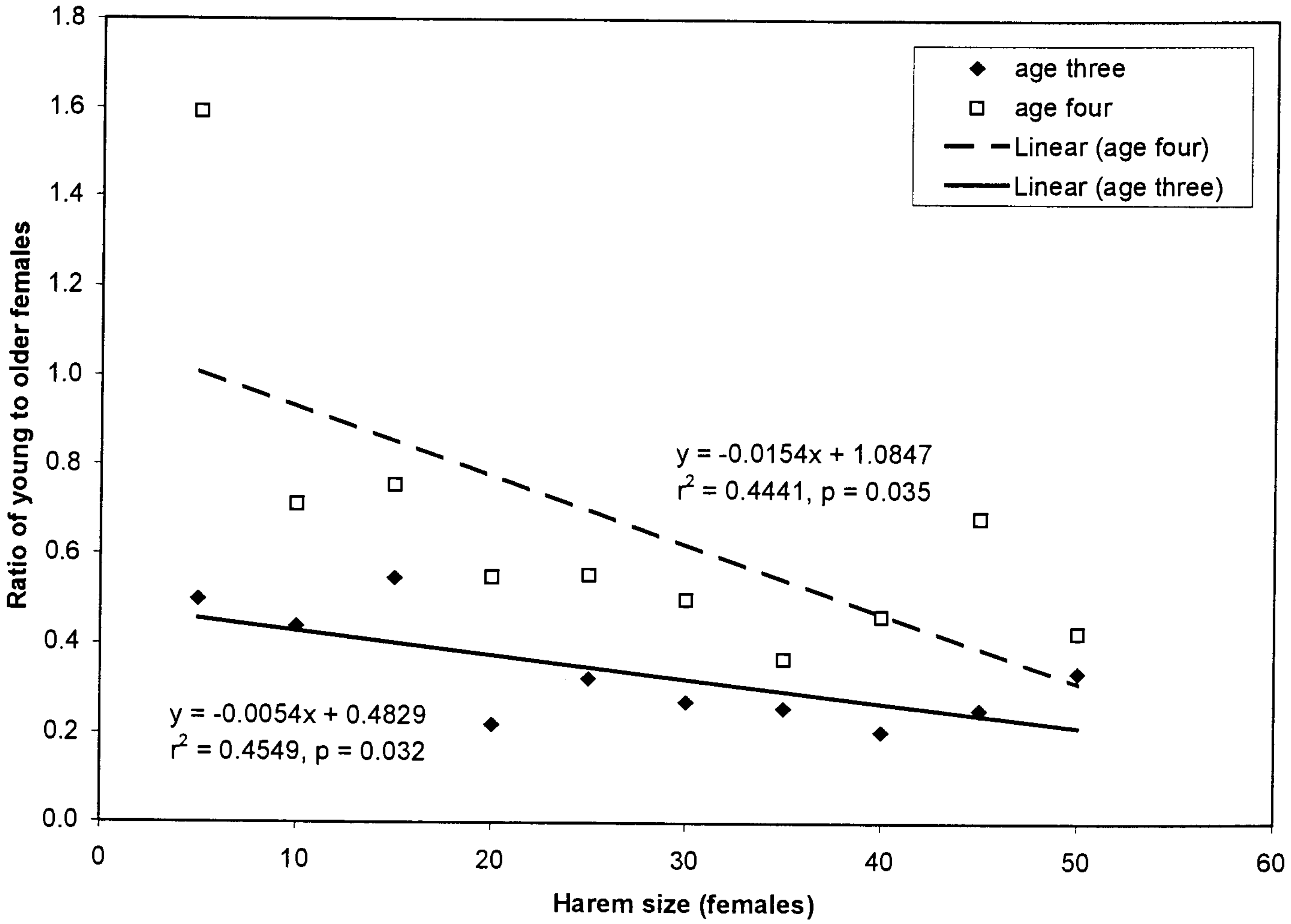

Figure 4. Inexperienced (ages 3 and 4) females expressed as a percentage of older (ages 6 and older) females in various sized harems at Marion Island.

3.4 Discussion

Pup mortality at Marion Island from 1990 through 1999 was slightly lower than that reported for southern elephant seals at South Georgia (4.5%, stable population; McCann 1985) and Macquarie Island (5%, declining population; Hindell & Burton 1987), slightly higher than at the small elephant seal population at Sea Lion Island in the Falklands (2.13%; Galimberti & Boitani 1999) and similar to that reported for Marion Island from 1986 through 1989 (3.6%; Wilkinson 1992). Pup mortality at Marion Island was similar to that reported for northern elephant seals at the largest colonies (Stewart 1989) but low compared to the smaller colony at Año Nuevo Island (range of 13-40%; Le Boeuf & Briggs 1977) where the influence of winter storms may greatly influence pup survival independent of number or density of breeding females (e.g., Stewart 1989, 1992).

Several factors may affect pre-weaning mortality of elephant seals particularly congenital problems causing stillbirths, abandonment leading to starvation, adult aggression in the rookery leading to physical injury and trauma, and the nature and topography of the breeding habitat (Le Boeuf & Briggs 1977; Reiter *et al.* 1978; Stewart 1989, Bester & Lenglart 1982; Wilkinson 1992; Hindell *et al.* 1994). We have rarely observed stillbirths at Marion Island. Moreover, beaches where most seals breed are generally wide enough to allow females to move further inland during heavy storms when surf may wash the lower parts of the beaches where females initially settle. Separation of pups from mothers, aggression of adult males and females, and topography of the breeding habitat may consequently be the most important factors resulting in deaths of nursing pups at Marion Island.

The inter-annual variability in pup mortality that was observed could be a consequence of several factors. In one year (1995) 16 pups died in a single harem (accounting for almost the entire year's mortality), which evidently resulted from aggressive behaviour of a young beach master. The composition of adult males in a given year is therefore likely to influence the level of pup mortality. The frequency and size of storms in a particular year could also influence pup mortality in a specific year.

Le Boeuf & Briggs (1977) suggested that pup mortality increased as births increased in northern elephant seals in the colony at Año Nuevo Island in Central California. Stewart (1989, 1992), however, found that pup mortality was independent of births at the substantially larger colonies in Southern California. Moreover, Stewart (1989, 1992) found no evidence for density-dependent pup mortality in the data reported by Le Boeuf & Briggs (1977) for Año Nuevo Island, but rather that patterns of mortality were independent of births or number of breeding females and was influenced by the timing and severity of winter storms there which resulted in high mortality in some years, regardless of colony size. Similarly, we found pre-weaning pup mortality to be independent of female density. In addition, we found no evidence for compensatory changes in pup survival as the population declined. This is not necessarily surprising as mortality was consistently low and evidently due to factors that affect pup health and survival regardless of population size. Separation of young pups from their mothers was certainly a contributing factor at Marion Island, as it is for elephant seals elsewhere (e.g., Le Boeuf & Briggs 1977; Bester & Lenglart 1982; Stewart 1989, Wilkinson 1992, Hindell *et al.* 1994). Trampling and disturbance of pups by breeding males is one agent of mother-pup separation (Carrick & Ingham 1962; Le Boeuf & Briggs 1977, Bester & Lenglart 1982), though it may not directly cause pup mortality by physical injury (Stewart 1989). Pups may, however, be suffocated when adult males come to rest on top of pups for several minutes or more (pers. obs.) but this evidently is not a significant factor in mortality overall.

We found that pup mortality was highest at sites where there were small numbers of females ashore at peak season. During our study, most of the females at those sites were young, small females, many giving birth for the first time. The higher mortality of pups of these females is evidently related to their inexperience, which may increase the chances that they and their pups become separated (cf Reiter *et al.* 1991 for northern elephant seals). Some of these sites may also be less protected from storm effects (Wilkinson *et al.* 1987). We think that these females may be excluded at times from more populated, perhaps more suitable habitats which are composed of older, larger, more experienced, and more aggressive females.

The smaller harems also often appeared to be dominated by younger males (pers. obs.). Frequent disturbance by young, less experienced males that attempt to mate with females, particularly non-receptive females with young pups, has been found to be a key factor in separation of mothers and pups and subsequent pup mortality among northern elephant seals (e.g., Stewart 1989). This behaviour in young adult males may also increase the number of pups that die from crushing and suffocation. Evidently it may be a key density-independent factor affecting pup survival at Marion Island. It is important to note that pup mortality in southern elephant seals could potentially be density-dependent at sites where southern elephant seals occur at higher densities.

In sum, we found that pre-weaning pup mortality has been consistently low, averaging less than 4% during the past 14 years at least, and that it has been constant regardless of number of births and number of females at peak season (as an index of density). Moreover, we found no evidence of a compensatory increase in pup survival as the population declined, also arguing against density-dependent influences on pre-weaning pup survival. The exceptions to particularly high pup survival were at beaches occupied by small numbers of young, inexperienced and primiparous females, which may also have been occupied by younger adult males that may cause greater disturbance to mothers and pups than at other sites. Consequently, changes in pre-weaning pup survival can not account for the decline in the Marion Island elephant seal colony in recent years, owing to the relatively constant and consistently high survival of pups to weaning.

CHAPTER 4 JUVENILE SURVIVAL AND POPULATION REGULATION IN SOUTHERN ELEPHANT SEALS AT MARION ISLAND

4.1 Introduction

A great deal of research has in recent years been aimed at demographic aspects of various southern elephant seal (*Mirounga leonina*) populations. The focus has in particular been on changes in population sizes (Hindell & Burton 1987; Guinet *et al.* 1992; Bester & Wilkinson 1994; Pistorius *et al.* 1999b), and causal factors contributing to these changes, both proximate and ultimate (Hindell 1991; Bester & Wilkinson 1994; Pistorius *et al.* 1999a). This emphasis on population dynamics has by and large been a result of the diminishing numbers of southern elephant seals over virtually their entire range in the southern Indian and Pacific Oceans during the past several decades (Bester & Lenglart 1982; Burton 1986; Hindell & Burton 1987; Guinet *et al.* 1992; Bester & Wilkinson 1994). Several of these populations now appear to have stabilised, or are thought to be in the process of stabilising (Guinet *et al.* 1999; Pistorius *et al.* 1999b).

The Marion Island elephant seal population has declined by 83% since 1951 (Laws 1994) and by 37.2% from some 2120 individuals in 1986 to 1330 individuals in 1994 at an average of 5.8% annual rate of change, which was linear over the period (Pistorius *et al.* 1999b). An intensive long-term mark-recapture study, which commenced in 1983, suggested the relatively low adult female survival as the proximate cause, and food limitation as deduced from the decline in survival of elephant seals with comparatively high energetic demands (first time reproductive costs in females and growth spurts in males), as the ultimate cause behind the population decline (Pistorius *et al.* 1999a). The study also discounted juvenile survival as contributing to negative growth of the population (Pistorius *et al.* 1999a). This inference was made by comparing juvenile survival at Marion Island with that of other elephant seal populations, including those for the South Georgia and Macquarie Island populations. Under the circumstances an inter-population comparison of juvenile survival was the only means by which to deduce the influence of this population component on population growth.

The comparison was, however, less than optimal in several respects. Demographic data from the stable South Georgia population was cross-sectional (rather than longitudinal) in nature and derived from a small sample size (see Caughley 1977; Pistorius *et al.* 1999a). This method of obtaining survival data has in recent years been increasingly criticised because of the assumptions that are made (e.g., stability of age structure, random sampling, and stationary population size over time) (Gaillard *et al.* 1993; Loison *et al.* 1994), despite it often being the only practical means of obtaining survival estimates for a population. Juvenile survival at Marion Island (Pistorius *et al.* 1999a) was similar to that for the Macquarie Island population (McMahon *et al.* 1999), which was also undergoing a population decline. Similar causative factors have been suggested for the decline in the two populations and the comparison was therefore largely inconsequential for the purpose of estimating the relative importance of juvenile survival in population growth.

The Marion Island population has been stable since 1994 (Chapter 5). Thus, the availability of recapture data for the population prior to 1994 (while in a state of decline) and from 1994 onwards (after the stabilisation) provides an opportunity to reliably quantify the influence that juvenile survival had on population growth at Marion Island. This latter comparison is the aim of this study. In this study we define juvenile survival as post-weaning survival over the first three years of life.

4.2 Methods

A total of 6940 (average: 498 annually, range: 396-686) elephant seal pups were double tagged in their hind flippers after weaning from 1983 to 1996 on Marion Island, using uniquely numbered, colour-coded Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom) (for more detail see Pistorius *et al.* 2000). For the period 1983-2000 all the beaches (32 along a 51.9-km coastline) were searched for tagged seals every 10 days during the moulting period (mid-November to mid-April) and, since 1990, also every 10 days during the winter (June, July and August). For each tagged seal that was resighted, attempts were made to record the tag number and colour combination, the number of tags remaining (one or two) and date of sighting. The resight data were entered and stored electronically in a database.

Encounter-history matrices, which are required for capture-mark-recapture analyses, were constructed from the resight data of males and females separately for the 1993 to 1996 cohorts, treating multiple sightings at a particular age as a single sighting. Seals were assumed to age by one year on 15 October which is the peak haulout date for adult females giving birth at Marion Island (Condy 1978; Bester & Wilkinson 1994). Resight data up to the year 1999 were used, which yielded 6 years of recapture data for the 1993 cohort and 3 years for the 1996 cohort. The software program MARK (G. White, Colorado State University; White & Burnham 1999), which is an application for the analysis of encounter-history matrices of marked individuals, was used to obtain likelihood estimates of annual survival and resighting probabilities of juveniles. The software program provides parameter estimates under the essential Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965), but also under several models that appear as special cases of this model (Lebreton *et al.* 1992). As it was impossible to distinguish mortality from permanent emigration in our study, we refer to apparent rather than absolute survival.

The two fundamental parameters in these models are: Φ = the survival probability for all animals between the ith and $(i + 1)$th encounter occasion ($i = 1, \ldots, k-1$), and p = the resighting probability for all animals in the ith encounter occasion ($i = 1, \ldots, k$).

The first step in the mark-recapture analysis involved Goodness of Fit (GOF) tests of the CJS model (full time-dependent model) for each cohort separately using the program RELEASE (Burnham *et al.* 1987) to check whether the assumptions pertaining to the model were met (see Lebreton *et al.* 1992). As age dependence was assumed, and the different cohorts were treated separately, Test 3.Sm was retained (see Lebreton *et al.* 1992).

We subsequently combined the recapture data for males and for females from the various cohorts for later analysis. To test whether there were any sex-specific differences in survival over the first three years we started off with a model incorporating recapture data from two groups, males and females. A Likelihood ratio test (LRT) between a model with separate age specific survival parameters for the two sexes and a model with similar parameters were used to test for a significant difference (see results). The data from both sexes were subsequently pooled.

Proper model selection, which is the primary issue in the analysis of capture-mark-recapture (CMR) data (Anderson *et al.* 1994), was accomplished using the Akaike Information Criterion (AIC; Akaike 1974). AIC is a standard procedure for model selection in a CMR context, and it weighs the quality of fit or deviance (defined as the difference in –2Log (Likelihood) of the current model and –2Log(Likelihood) of the saturated model) and the precision (via the number of parameters), so as to select the most parsimonious model that adequately describes the data (Lebreton *et al.* 1993; Anderson *et al.* 1994; Loison *et al.* 1994). It was used to select between a model with age-specific, time-specific, age- and time-specific and constant capture- and survival probability.

Juvenile survival during the population decline (taken from Pistorius *et al.* 1999a) was averaged over the period (cohorts 1983-1992) and compared to survival after the decline in order to quantify its response to the population stabilisation. We tested whether there was a significant change in first, second and third year survival using a Mann-Whitney U test (two-tailed). We used annual survival estimates obtained from separate cohort models for this purpose (from this study and from Pistorius *et al.* 1999a). Juvenile survival was described separately for the two sexes in Pistorius *et al.* (1999a) and we averaged the estimates for males and females prior to performing the test.

Elephant seals at Marion Island have been tagged in both flippers since the commencement of the mark-recapture program in 1983. This has allowed for the assessment of the potential for bias in estimates of survival rates resulting from tag loss and estimation of correction factors to compensate for tag loss. Although tag loss rates in adult elephant seals become reasonably high, that for juveniles is very low with an annual range of 1.3 - 2.4 percent single tag loss (Pistorius *et al.* 2000). Nonetheless, cumulative age-specific tag retention rates were used to adjust the survival estimates to compensate for tag loss (Pistorius *et al.* 2000).

4.3 Results

The CJS model did not fit the data for the majority of cohorts (Table 2), suggesting violation of the underlying assumptions of the model. Data from males and females from the 1993 cohort showed a reasonably good fit but all the other data sets showed departures from the CJS model.

We tested for a gender-effect on survival and found no significant difference between male and female survival (χ^2 = 2.84, df = 3, p = 0.417) of juvenile elephant seals, which allowed pooling of the recapture data from the two sexes. The constant resighting probability model proved to be more parsimonious than the age and/or time dependent resighting probability model as would be expected from resighting data that was collected through constant search effort (Table 3). Survival of southern elephant seals over the first three years of life were clearly age-dependent (AIC = 7023.39 vs AIC = 7129.51; Table 3). We found no significant inter-annual differences in survival over the study period (χ^2 = 12.56, df = 7, p = 0.084; Table 3), suggesting that juvenile survival over the first three years has been reasonably constant, at least since the halt in the population decline.

Juvenile survival reported in this study was very similar to estimates obtained while the population was declining (Table 4). First year survival was 1.2% lower, and second and third year survival 3.3% and 1.8% higher in the latter period with an average increase of 1.7% concurrent with the halt in the population decline. There was nonetheless no significant change in first ($p = 0.733$), second ($p = 0.190$), or third ($p = 0.345$) year survival concurrent with the stabilisation of the elephant seal population. Juvenile survival therefore does not appear to have been affiliated to the population decline at Marion Island or to be a major regulating agent in the population.

Table 2. Goodness-of-fit tests of the Cormack-Jolly-Seber model by southern elephant seal cohort (1993-1996) and sex for the Marion Island population (for 1994 females and 1995 males results from Test 3.Sm and Test 3 were very similar and results from the latter is provided).

Cohort		*Males*			*Females*	
	$\chi2$	*df*	P	$\chi2$	*df*	*P*
1993	3.33	3	0.344	4.47	3	0.215
1994	6.04	1	0.014	11.76	5	0.040
1995	16.25	3	0.001	3.12	1	0.077
1996	8.61	1	0.003	3.36	1	0.067

Table 3. Elimination of nonsignificant effects from the full CJS model in modelling juvenile survival and resighting probability in southern elephant seals from Marion Island: for each model the number of estimable parameters (np), the deviance (DEV), and the Akaike information criterion (AIC) are given.

Model	*np*	*DEV*	*AIC*
(1) (ϕa pc)	7	579.99	7023.39
(2) (ϕa,t, pc)	14	567.44	7024.91
(3) (ϕa, pa)	11	575.26	7026.69
(4) (ϕa, pt)	12	577.71	7031.16
(5) (ϕa, pa,t)	23	558.68	7034.34
(6) (ϕc1-3, pc)	5	690.13	7129.51

ϕ_a : Age-dependent survival probability; ϕ_t : Time-dependent survival probability

$\phi_{c1\text{-}3}$: Survival constant over first three years

p_a : Age-dependent resighting probability

p_t : Time-dependent resighting probability

p_c: Constant resighting probability

Table 4. Survival (ϕ) and resighting (p) probabilities of southern elephant seal juveniles from Marion Island during and after the population decline (survival estimates corrected for tag loss). Estimates from the 1983-1992 cohorts while the population was declining are taken from Pistorius *et al.* (1999a).

Year	ϕ	*S.E.*(ϕ)	p
1	0.595	0.013	0.769
2	0.814	0.017	0.769
3	0.781	0.020	0.769
	Average 1983-1992		
1	0.607	0.036	0.699
2	0.781	0.049	0.707
3	0.763	0.058	0.697

4.4 Discussion

Juvenile survival is often thought to be a key component of population dynamics and a potential indicator of population status in large-mammal populations (Eberhardt & Siniff 1977; Eberhardt 1981; Promislow & Harvey 1990; Hindell *et al.* 1994; York 1994; Benton *et al.* 1995; Jorgenson *et al.* 1997). In pinnipeds, studies of juvenile survival are thought to be of major importance to their conservation (Hastings *et al.* 1999), since this parameter has the potential to greatly influence population growth (Eberhardt & Siniff 1977). Declines in several pinniped populations have been attributed to decreased juvenile survival (Trites & Larkin 1989; Hindell 1991; York 1994). In the present study juvenile survival did not show significant changes with the stabilisation of a declining population of elephant seals. Survival of this population component therefore appears to have been inconsequential in the population decline at Marion Island (also see Appendix 2).

When evaluating the data in terms of meeting the underlying assumptions of the CJS model, the majority of cohorts failed to pass the GOF test, suggesting heterogeneity in survival and/or capture probability within groups of individuals last released on the same sampling occasion. We suspect survival to be homogenous amongst individuals, although size, and therefore condition at weaning clearly influence first year survival rates at Macquarie Island (McMahon *et al.* 2000). Heterogeneity in resighting probability is very likely to be the reason for the departures as juveniles are less philopatric than adults (Hofmeyr 2001), and have recently been shown to exhibit differential levels of philopatry (Chapter 9). This heterogeneity (in resighting or survival probabilties) is often encountered in real data sets and it results in relatively small if any biases on survival rates since the analysis methods used have some robustness to heterogeneity (Carothers 1979; Nichols *et al.* 1982; Pollock & Raveling 1982; Burnham *et al.* 1987). It may, however, result in actual variances of estimates exceeding estimated theoretical variances (Burnham *et al.* 1987) and this does form a weakness in the present study. Our sample size of tagged elephant seals were fortunately particularly large and we consequently obtain very low standard errors, that if even doubled would not have been excessively high (e.g., Gaillard *et al.* 1993; Jorgenson *et al.* 1997; Hastings *et al.* 1999). As the present mark-recapture program is based on an extremely rigorous resighting protocol, we expect that if any estimate bias occurred, that it would have been constant throughout the study period. It would therefore not have weakened the confidence placed on the comparison of estimates and on hypothesis testing (i.e., presence of inter-annual variability in estimates) within the study.

Juvenile survival in large mammals have been concluded to be much more sensitive to density dependence and external influences than adult survival, with the latter being buffered against density effects (Fryxell 1987; Owen-Smith 1990; Gaillard *et al.* 1998). Based on observations from 24 populations of 16 species of large mammals, Gaillard *et al.* (1998) also maintained that survival of prime-aged females showed little among-year variation (CV varying from 2 to 15%). In contrast, juvenile survival showed marked temporal variation in 19 populations of 14 species (CV varying from 12 to 88%). The present study and results from Pistorius *et al.* (1999a) provide opposing evidence for southern elephant seals. Juvenile survival appeared unaffected by population density with adult female survival being density dependent. A recent study demonstrated that variation in survival was also substantially higher for adults than juveniles (Pistorius *et al.* 1999a).

Although the foraging ranges of some adult male and female southern elephant seals from Marion Island have been documented (Bester 1989; Jonker & Bester 1998; Malherbe 1998), those for juveniles remain relatively poorly documented. A possible explanation for the dichotomy in survival patterns between juveniles and adults could be separate foraging grounds (Bornemann *et al.* 2000). Under similar foraging conditions, absolute energy requirements would also be significantly less for juveniles, and if prey items are equally available to juveniles and adults, the latter component would be more susceptible to food limitation.

No gender effect on juvenile survival was apparent from this study. Greater mortality in males is often related to sexual selection (Fisher 1930) because of the larger male morph and polygyny (Clutton-Brock *et al.* 1982; Pistorius *et al.* 1999a), and this have been demonstrated for adult elephant seals at Marion Island (Pistorius *et al.* 1999a). Juvenile males and females are relatively similar in body size (see Carrick *et al.* 1962; McLaren 1993). The absence of a gender effect in these animals is therefore expected. Higher female survival has, however, recently been documented for juvenile Weddell seals (Hastings *et al.* 1999b).

Adult female survival explicitly responded to population growth rate in the southern elephant seal population at Marion Island, as has been demonstrated for a few other mammal populations including Alpine ibex and porcupine caribou (Eberhardt 1985; Walsh *et al.* 1995; Toigo *et al.* 1997). We therefore conclude that adult female survival, rather than juvenile survival, is the major regulating agent in the Marion Island population (see Appendix 2). Similar causative factors have been proposed (Hindell *et al.* 1994) for the declines of southern Indian and Pacific Ocean southern elephant seal populations (including Îles Kerguelen and Macquarie Island), and the above conclusion about adult female survival may therefore be relevant to these populations.

CHAPTER 5 EVIDENCE FOR POPULATION STATUS AS A FUNCTION OF ADULT FEMALE SURVIVAL

5.1 Introduction

The significance of the various demographic variables and their respective potential contributions to population change forms an important issue in population ecology (Eberhardt & Siniff 1977; Eberhardt 1981; Promislow & Harvey 1990; Gaillard *et al.* 1998). Population size responds directly to changes in age-specific survival and fecundity (Jorgenson *et al.* 1997). Accurate measures of these parameters are difficult to acquire since they necessitate long-term monitoring of known aged individuals. Demographic parameters are expected to vary according to age in populations that are age-structured (as is the case in most vertebrates), and these demographic parameters have different consequences for population dynamics (Krebs 1985). Although several studies have quantified survival rates for specific populations, very few have compared these rates among populations growing at different rates to assess their effects on population status and trends. Studies on adult survival in large mammals are particularly sparse due to the required long-term monitoring of many marked individuals to obtain accurate estimates and this is consequently a major limitation in understanding population regulation, despite its importance from both management and evolutionary viewpoints.

Elephant seals are particularly immobile on land compared with most other large mammals, and this greatly facilitates the ease with which they are marked and recaptured (physically or by visual inspection). This and the fact that long-term studies have been made of several southern elephant seal colonies allows good comparisons of vital rates within and among populations.

The focus of much recent demographic study of southern elephant seals (*Mirounga leonina*) has been on population trends (e.g., Hindell & Burton 1987; Guinet *et al.* 1992; Bester & Wilkinson 1994; Pistorius *et al.* 1999b) and on identifying proximate and ultimate causes of variation in population size (Hindell 1991; Bester & Wilkinson 1994; Pistorius *et al.* 1999a). A key concern has been the long-term decline of southern elephant seals throughout the southern Indian and south Pacific oceans (van Aarde 1980; Burton 1986; Hindell & Burton 1987; Guinet *et al.* 1992; Bester & Wilkinson 1994). Several of these populations have apparently stabilised subsequently, or thought to be in the process of stabilising (Guinet *et al.* 1999; Pistorius *et al.* 1999b).

The southern elephant seal population at Marion Island declined by 83% since 1951 (Laws 1994). It declined about 37% between 1986 and 1994 (5.8% annual rate of decline) from 2120 to 1330 seals (Pistorius *et al.* 1999b). Results of long-term mark-recapture studies have suggested that this decline has been due to low survival of adult females. A decline in prey availability is thought to be the ultimate cause (Pistorius *et al.* 1999a).

The southern elephant seal population at Patagonia (Peninsula Valdés, Argentina) numbers around 43 300 (Lewis *et al.* 1998) and is the only population that has clearly increased since 1951 (Campagna & Lewis 1992; Laws 1994). It increased at 5.1% annually from 1975 through 1982 and 3.6% annually since (Lewis *et al.* 1998).

The aims of this study were to: (a) determine trends in the elephant seal population at Marion Island since 1994, (b) estimate survival of adult females at Marion Island, and (c) compare it with survival data for adult females at Marion Island prior to 1994 and at the increasing population at Peninsula Valdés in Patagonia.

5.2 Methods

5.2.1 Study sites

Marion Island (46°54'S, 37°45'E), one of two islands in the Prince Edward Island group, is located in the sub-Antarctic region of the southern Indian Ocean, approximately 2180 km SSE of Cape Town, South Africa (Fig.1). Its size is roughly 290 km^2 with a coastline of approximately 90 km, dominated by volcanic bluffs separating small boulder and pebble beaches (Wilkinson 1992). Seals mainly haul out on easterly beaches (Condy 1978). Peninsula Valdés (42°30'S, 64°W) is on the east coast of Patagonia, Argentina, and along the temperate waters of the south Atlantic Ocean (Fig.1). Elephant seals haul out and breed there along 200 km of pebble and sandy beaches (Campagna & Lewis 1992).

5.2.2 Data collection

In this study we compare adult female survival between the elephant seal population at Marion Island and the one at Peninsula Valdés. The survival estimates for the two populations are derived from two different types of data sets. At Marion Island the elephant seals were marked as pups allowing estimation of age-specific vital rates, whereas females at Peninsula Valdés were tagged as adult females of unknown age. In comparing the two populations we will therefore make use of average adult survival rather than age-specific survival.

5.2.3 Marion Island

We tagged 3070 (average: 256 annually, range: 198-343) weaned female elephant seal pups in each of their hind flippers between 1983 and 1994 on Marion Island, using uniquely numbered, colour-coded Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom) (see Pistorius *et al.* 2000 for details). We searched for tagged seals at all the beaches (32 along a 51.9-km coastline) on the island every seven days during the breeding season (mid-August to mid-November) and every 10 days during the moulting period (mid-November to mid-April) each year from 1983 to 1999 and every 10 days during the winter (June, July and August) since 1990. We recorded the tag number and colour combination of each tagged seal during these surveys.

5.2.4 Peninsula Valdés

At Peninsula Valdés most tagging of seals was done along 11 km of beaches in the area of Punta Delgada. Resighting efforts were also focused there, although a larger area of about 31 km was searched less often. The mark-recapture study site is located within the most concentrated section of the population's distribution on the peninsula. A total of 804 adult females were marked during the breeding season from 1990 through 1994 at Punta Delgada (1990: n=243; 1991: n=36; 1992: n=19; 1993: n=60; 1994: n=446). Only females with pups or females that were visibly pregnant were tagged. We did not know the exact ages of any of these sexually mature females. Colour coded and uniquely numbered Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom) were applied to the inter-digital webbing of either one or two hind flippers of the seals. For each year of tagging the proportion of single and double-tagged seals were recorded. Since 1990 the Punta Delgada area was traversed by foot on a weekly basis during the breeding seasons and tag numbers and colours of resighted seals were recorded, yielding eight years of recapture data for animals tagged in 1990 and four years for those tagged in 1994.

5.2.5 Data analyses

We regressed population size at Marion Island on time to determine trends in abundance from 1994 through 1999. Annual estimates of population size prior to 1998 and methods used to calculate population size for 1998 and 1999 are described by Pistorius *et al.* (1999b).

Encounter-history matrices, which are required for capture-mark-recapture analysis, were constructed from the resight data, treating multiple sightings in a year as a single sighting. Seals were assumed to age by one year on 15 October and 2 October which is the peak haul-out date for adult females at Marion Island and Peninsula Valdés respectively (Condy 1978; Bester & Wilkinson 1994; Campagna *et al.* 1993). The software program MARK (G. White, University of Colorado), which is an application for the analysis of marked individuals, was used to obtain likelihood estimates of survival and capture probability using the above-mentioned matrices. The software program provides parameter estimates under the essential Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965), but also under several models that appear as special cases of this model (Lebreton *et al.* 1992). As it was impossible to distinguish mortality from permanent emigration in our study, we refer to apparent rather than absolute survival.

The two fundamental parameters in these models are:

Φ = the survival probability for all animals between the *i*th and $(i + 1)$th sample ($i = 1, \ldots, k - 1$), and p = the capture probability for all animals in the *i*th sample ($i = 1, \ldots, k$).

The first step in the mark-recapture analyses involved Goodness of Fit (GOF) tests of the CJS model (full time-dependent model) using the program RELEASE (Burnham *et al.* 1987) to validate the model assumptions (see Lebreton *et al.* 1992). As age dependence was assumed, and the different cohorts were treated separately, Test 3.Sm was retained for the Marion Island data (see Lebreton *et al.* 1992). Adult females marked at Peninsula Valdés were not expected to demonstrate age-dependence and the full GOF tests were used to test assumptions pertaining to the CJS model.

Proper model selection, which is the primary issue in the analysis of capture-mark-recapture (CMR) data (Anderson *et al.* 1994), was accomplished using the Akaike Information Criterion (AIC). AIC is a standard procedure for model selection in a CMR context, and it weighs the quality of fit (deviance) and the precision (via the number of parameters), so as to select the most parsimonious model that adequately describes the data (Lebreton *et al.* 1993; Anderson *et al.* 1994; Loison *et al.* 1994). It was used to select between the full-time dependent model and the constant-capture-probability model (assuming no year-to-year changes in capture probability) for each Marion Island cohort as well as for the Peninsula Valdés females. The model with the lowest AIC value was selected for each cohort and group. Survival rates in large mammals are expected to plateau after first reproduction (Caughley 1977). Survival probabilities from the Peninsula Valdés adult females were therefore kept constant (as they were marked as adults). If this reduced the AIC value further, the model was selected.

Cumulative age-specific tag retention rates, estimated from double-tagged individuals (Pistorius *et al.* 2000), were used to adjust the survival estimates from females at Marion Island to compensate for tag loss. Due to insufficient tag loss data from the Peninsula Valdés population and the inability to differentiate between various age classes, the survival estimates for this population were corrected using the average annual tag loss rate for adult females in their fifth to tenth year at Marion Island (3% single tag loss) to estimate cumulative tag retention.

Analysis of the population data from Marion Island revealed that numbers decreased continuously from 1986 to 1994 and stabilised thereafter (see Results, Fig. 1). Therefore, the Marion Island age-specific survival estimates before 1994 (taken from Pistorius *et al.* 1999a) were pooled to represent the declining population and all the estimates after 1993 (Pistorius *et al.* 1999a; present study) were pooled to represent the stable population. The latter estimates were obtained from 12 cohorts, 1983-1994. These pooled estimates were compared with each other in order to quantify differences in age-specific survival estimates associated with the stabilisation of the population. We averaged estimates of females older than 4 years to allow comparisons of survival of adult females from the two populations.

5.3 Results

We found no change in population size at Marion island from 1994 through 1999 ($y = -2.57x + 1366$, $r^2 = 0.02$, $p = 0.79$) suggesting that the population was stable during this period (Fig 1).

The CJS model fitted the data for all the cohorts from Marion Island except for the 1991 cohort (Table 5). The model fitted the data from the Peninsula Valdés females satisfactorily according to Test 3.Sm (Table 5).

The constant capture probability model was more parsimonious than the full time-dependent model for all Marion Island cohorts (Table 6). For the Peninsula Valdés females the most parsimonious model was fully time dependent (Table 6). Survival estimates and capture probabilities are presented in Table 7 and a comparison between the age-specific survival estimates from Marion Island during and after the population decline in Table 8.

Although survival probabilities of several female age classes at Marion Island were higher after than during the decline, the significant ($\chi^2 = 18.06$, df = 3, $p < 0.001$) increase in survival probabilities of prime-age females (ages 4, 5 and 6 which contribute more than 50% to the reproductive schedule (Pistorius *et al.* 1999b)) were by far the most noteworthy (average increase of 8%).

Adult females from Peninsula Valdés had an average survival rate of 84.2%. This was approximately 6% higher compared to that for females 5 years and older in the stable Marion Island population.

Table 5. Goodness-of-fit tests of the Cormack-Jolly-Seber model by southern elephant seal cohort for the Marion Island population and adult females tagged in 1990-1994 at Peninsula Valdés.

Cohort	χ^2	*df*	*P*
		Marion Island	
1991	17.41	3	0.001
1992	2.69	2	0.261
1993	4.47	3	0.215
1994	8.13	5	0.149
		Peninsula Valdés	
Adult females	4.04	4	0.401

Table 6. Elimination of nonsignificant effects from the full CJS model in modelling survival probability in southern elephant seals from Marion Island and Peninsula Valdés: for each model the number of estimable parameters (np), the deviance (DEV), and the Akaike information criterion (AIC) are given.

Cohort	*Model*	*np*	*DEV*	*AIC*
		Marion Island		
1991	(1) (ϕ_t, p_t)	15	334.72	1679.87
	(2) (ϕ_t, p_c)	9	336.49	**1669.24**
1992	(1) (ϕ_t, p_t)	13	226.07	1304.58
	(2) (ϕ_t, p_c)	8	227.94	**1296.09**
1993	(1) (ϕ_t, p_t)	11	157.04	1124.04
	(2) (ϕ_t, p_c)	7	158.25	**1116.99**
1994	(1) (ϕ_t, p_t)	9	67.54	922.97
	(2) (ϕ_t, p_c)	6	67.79	**917.01**
		Peninsula Valdés		
Adult females	(1) (ϕ_t, p_t)	15	385.62	**3783.59**
	(2) (ϕ_t, p_c)	9	434.96	3820.75
	(3) (ϕ_c, pt)	9	483.72	3869.51

ϕ_t : Time-dependent survival rate; ϕ_c: Constant survival rate
p_t: Time-dependent capture probability; p_c: Constant capture probability

Table 7. Survival (ϕ) and capture (p) probabilities of southern elephant seals from Marion Island and Peninsula Valdés.

Year	*ϕ*	*S.E.(ϕ)*	*p*	*ϕ*	*S.E.(ϕ)*	*p*
			Marion Island			
	Cohort 1991			Cohort 1992		
4	0.789	0.049	0.711	0.811	0.054	0.737
5	0.869	0.049	0.711	0.790	0.062	0.737
6	0.895	0.031	0.711	0.795	0.055	0.737
7	0.903	0.031	0.711			
	Cohort 1993			Cohort 1994		
4	0.899	0.047	0.785	0.813	0.064	0.784
5	0.756	0.059	0.785			
			Peninsula Valdés			
	Adult females tagged in 1990-1994					
1991	0.856	0.044	0.408			
1992	0.856	0.047	0.595			
1993	0.947	0.046	0.583			
1994	0.860	0.043	0.648			
1995	0.727	0.024	0.783			
1996	0.751	0.036	0.586			
1997	0.896	0.058	0.706			

Table 8. Comparison of adult female survival in the southern elephant seal population at Marion Island while in a state of decline and after it has stabilised (survival estimates taken from present study and Pistorius *et al.* 1999a).

Age	*Declining average survival rate*	*Stabilised average survival rate*	*Difference*
3	0.820 (1986/87-1993/94)	0.828 (1994/95-1997/98)	+ 0.8%
4	0.746 (1987/88-1993/94)	0.814 (1994/95-1997/98)	+ 6.8%
5	0.757 (1988/89-1993/94)	0.803 (1994/95-1997/98)	+ 4.6%
6	0.737 (1989/90-1993/94)	0.864 (1994/95-1997/98)	+ 12.7%
7	0.755 (1990/91-1993/94)	0.775 (1994/95-1997/98)	+ 2.0%
8	0.762 (1991/92-1993/94)	0.780 (1994/95-1997/98)	+ 1.8%
9	0.781 (1992/93-1993/94)	0.718 (1994/95-1997/98)	- 6.3%
10	0.710 (1993/94)	0.740 (1994/95-1997/98)	+ 3.0%
6-10	0.749	0.775	+ 2.6%

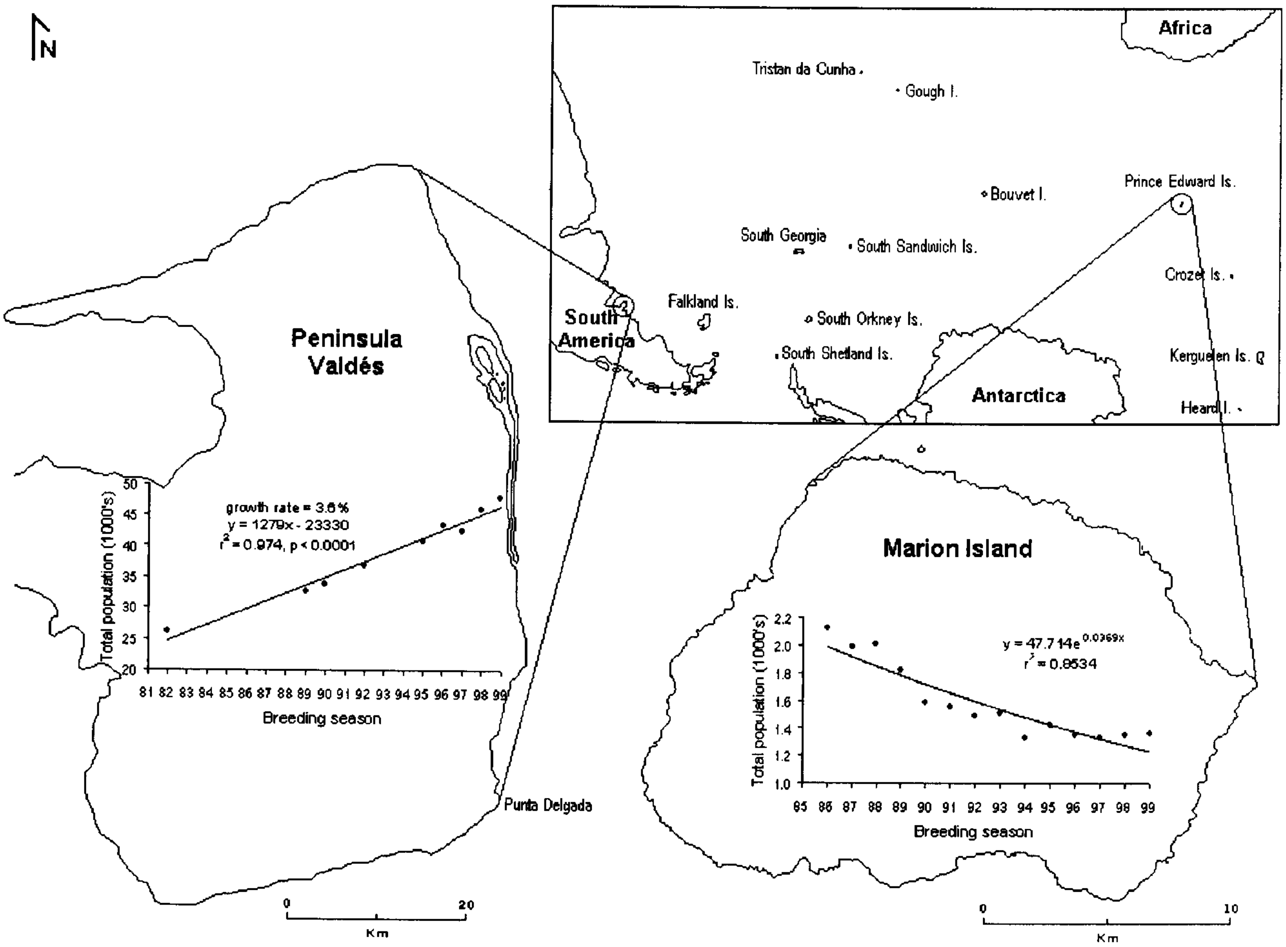

Figure 5. Growth of the southern elephant seal populations at Marion Island and Peninsula Valdés

5.4 Discussion

Factors that influence population growth, and explain variation in growth rate between populations, are of major interest in population ecology for both practical and theoretical reasons (Gaillard *et al.* 1998). Studies that can identify what shifts in vital rates are required to influence changes in population size are of particular interest for life history theory, wildlife management and conservation biology (Caughley 1977; Gaillard *et al.* 1998). Comparing vital rates between populations with varying growth rates is required in order to quantify changes in these rates that influence population change.

The general approach used to obtain the demographic data whereupon this study is based, was analogous for the Marion Island and Peninsula Valdés populations (mark-recapture rather than cross-sectional). This permits comparison of vital rates between the two populations, subject to limitation imposed by a difference in the methods (see Methods). The difference in methodology used resulted in one data set (Marion Island) being age-specific, and the other distributed over all adult female age classes.

To overcome this limitation, we averaged the age-specific estimates from Marion Island to facilitate comparison of adult female survival between the two populations. As female numbers diminish in each consecutive age class, averaging of age-specific survival estimates may be considered unrepresentative of true overall adult female survival. However, as survival of females plateau once breeding status is attained and is relatively constant over time (Caughley 1977; Gaillard *et al.* 1998; Pistorius *et al.* 1999a) we assume that the average adult female survival estimate for Marion Island was unbiased and the comparison between the two populations valid.

A site-specific rate of tag loss could not be calculated for Peninsula Valdés, and if tag loss rates were lower at this site than at Marion Island, then using a conversion based on tag loss rates calculated for Marion Island, would produce an overestimate in adult survival. A major contributing factor to tag loss in southern elephant seals is the enlarging of the hole through which the shaft of the tag protrudes as a result of infection (Wilkinson & Bester 1997). Peninsula Valdés is situated further north relative to Marion Island resulting in a substantially warmer climate, and hence increased likelihood of wound infection. We therefore expect, if anything, that tag loss would be greater at Peninsula Valdés and the survival estimates from this site negatively biased.

When evaluating the data in terms of meeting the underlying assumptions of the CJS model, the Valdés adult female data set failed to pass the Test 2 component. This examines heterogeneity among "cohorts", where cohort is defined as the group of individuals last released on the same sampling occasion. Failing this test is therefore potentially a consequence of age dependence in survival and capture probabilities. This has been recognised and explained for the Marion Island data (Pistorius *et al.* 1999a). For the Valdés adult female data the failure is possibly a consequence of differences in survival and breeding intervals between first time breeders and the rest of the adult population. In studies where it is possible to distinguish between time-dependent and age-dependent survival (unlike the present study) it is possible to perform pseudo-GOF tests as described in Lebreton *et al.* (1992) and this test accounts for age dependence. The 1991 cohort from Marion Island failed the GOF test suggesting heterogeneity among individuals with different capture histories, and estimates from this cohort should be interpreted with relative caution. Departures from the CJS model generally do not affect point estimates of survival (Carothers 1979), but cause underestimation of standard errors of survival estimates (Burnham *et al.* 1987).

In the present study, rates of adult female survival displayed an explicit response to population growth rate as has been demonstrated for a few other mammal populations including Alpine ibex and porcupine caribou (Eberhardt 1985; Walsh *et al.* 1995; Toigo *et al.* 1997; see Appendix 2). An eight-percent increase in prime-age adult female survival was associated with a halt of a 5.8 % annual rate of decline at Marion Island, whereas a 5-6% higher adult female survival in the Peninsula Valdés population (compared to the stable Marion Island population) was associated with a 3.6% annual rate of increase.

A few previous studies have found that food availability apparently had a greater influence on adult than on juvenile survival (Sinclair *et al.* 1985; Fryxell 1987). There is considerably more evidence that juvenile survival is more strongly related to food availability (Clutton-Brock *et al.* 1982; Skogland 1985; Owen-Smith 1990; Jorgenson *et al.* 1997). Pistorius *et al* (1999a) suggested that the decline of the Marion Island elephant seal population has been ultimately related to food limitation. The results of this study support the notion that food availability has a greater influence on adult female than on juvenile survival, the latter remaining high even in declining elephant seal populations (Bester & Wilkinson 1994; Pistorius *et al.* 1999a; McMahon *et al.* 1999). Should energetic requirements of pregnant females, which include nourishment of the growing foetus and accumulation of sufficient fat reserves to wean her pup (Condy 1979; Oftedal *et al.* 1987; Carlini *et al.* 1997), outweigh those of juveniles, as suggested by Hastings *et al.* (1999) in a study of Weddell seals (*Leptonychotes weddellii*), this would explain why food limitation had a more pronounced affect on adult female than on juvenile survival. As mass at birth and weaning mass impact on first year survival of elephant seals (McMahon *et al.* 2000), and weaning mass is considered to be closely linked to female foraging success prior to parturition (Burton *et al.* 1997), one would expect a food mediated drop in adult female survival to impact on first year survival.

This could not be demonstrated for the Marion Island elephant seal population, first year survival remaining consistently high over all the years of study (Pistorius *et al.* 1999a). However, during the period of probable food limitation, southern elephant seal males have been shown to have a lower survival rate than females and this was ascribed to the increased energetic requirements of the larger male morph (Pistorius *et al.* 1999a). An alternative explanation for food limitation affecting adults rather than juveniles could potentially be separate foraging grounds, or different foraging strategies between the two population components. Such contrasting foraging constraints could also potentially mask the above-mentioned impact that food limitation applying to adult females would have on juvenile survival.

Although foraging ranges and diving behaviour of adult elephant seals at Marion Island and Valdés Peninsula have been investigated (Campagna *et al.* 1995; Campagna *et al.* 1998; Jonker & Bester 1998; Malherbe 1998; Campagna *et al.* 1999) juvenile foraging behaviour at these populations remains unknown. Slip (1997) has, however, provided evidence that these two population components utilise similar foraging ranges and strategies, at least at Heard Island, which points to the differential energy requirement hypothesis as a more likely explanation. On the other hand, the adults and juveniles might be exploiting different prey as very young elephant seals do not dive as deep (Thorson & Le Boeuf 1994), although by age two the dive pattern is similar to that of adults (Le Boeuf 1994).

Several studies have highlighted the difficulties associated with teasing apart the respective contribution of recruitment and adult survival towards population growth (Escos *et al.* 1994; Walsh *et al.* 1995 Gaillard *et al.* 1998). Recruitment can be measured as a combination of juvenile survival and the proportion of females breeding. Juvenile survival has been dismissed as a population component bringing about population change at Marion Island (Pistorius *et al.* 1999a). Breeding probabilities of Marion Island elephant seal females have, however, increased and their age of maturity has decreased during the period 1986 to 1997 (Pistorius *et al.* 2001). It follows that the combination of increased adult female survival and breeding probabilities has been instrumental in altering the trend of population growth at Marion Island, although the latter have had a small effect relative to adult female survival (Appendix 2).

In this study it was not possible to distinguish prime-age female survival from survival of all adult females at Peninsula Valdés. The results from Marion Island suggest that prime-age female survival is an important variable influencing elephant seal population status, and marking females as pups so as to allow estimation of age-specific survival at Peninsula Valdés, should therefore be a prerogative of future research. This step will also permit estimation of age of maturity and other reproductive rates for the population.

An important assumption made in this study is that marked animals do not permanently emigrate from the study sites, and are therefore not lost for potential recaptures. When using the above-mentioned models for mark-recapture analyses, permanent emigrations are functionally similar to mortalities, and result in negatively biased survival estimates. The estimates presented in this study would, moreover, be underestimated if permanent emigration did take place. Adult females have been shown to be highly philopatric with respect to their particular breeding beaches (Hindell & Little 1988; Bester 1989; Hofmeyr 2001), and we expect that permanent adult female emigration from our study areas was minimal. At Peninsula Valdés the mark-recapture site occupies only a small area of the coastline where elephant seals haul out and the above-mentioned effect is likely to be more substantial here relative to at Marion Island and may have resulted in negatively biased survival rates.

Eberhardt (1977) first postulated the widely accepted view that population regulation in large mammals commences with changes in survival of juveniles, followed by changes in the age of first reproduction and reproductive rates of females, and ultimately by shifts in adult survival. Research on the Marion Island elephant seal population has, however, indicated that reproductive rates was the first parameter to respond to environmental change (Pistorius *et al.* 2001) followed by changes in survival of prime-age females (present study), while juvenile survival remained high (Pistorius *et al.* 1999a).

CHAPTER 6 A LONGITUDINAL STUDY OF SENESCENCE IN A PINNIPED

6.1 Introduction

Three stages of survival are generally accepted for mammals, namely a juvenile stage with a low survival rate, a prime-age adult stage with a high survival rate, and a senescent stage with a decreasing survival rate (Caughley 1966; Eberhardt 1985). Juvenile and prime-age adult female survival has been thoroughly studied over a broad range of mammalian species. Senescence has by comparison been largely neglected and still remains a controversial phenomenon (Gaillard *et al.* 1994).

Senescence has been defined as the rate of increase in age-specific mortality with age, which results from degenerative changes in the organism (Abrams 1991; Promislow 1991). The existence of a senescence effect on survival is widely acknowledged for large mammals (Caughley 1966; Eberhardt 1985; Promislow 1991), although it has very seldom been demonstrated on statistical grounds (Gaillard *et al.* 1993; Jorgenson *et al.* 1997). In a comparative study using data compiled from 56 natural populations of mammals, Promislow (1991) found age-specific mortality in adults to increase in 46 populations with the increase being significant in 26 of these. The above finding was used as evidence supporting the pervasiveness of senescence in mammals.

On the other hand, Gaillard *et al.* (1994) reported on several biological and statistical flaws associated with the study of Promislow (1991) and argued against the validity of using the results as a basis by which to accept the occurrence of senescence in mammals. The major argument against the soundness of the conclusions reached by Promislow (1991) was based on the fact that mortality data from more than 86% of the populations considered were based on transversal life tables. In these cases strong assumptions that are commonly not met need to be satisfied to provide unbiased estimates, including stationary age distribution and an equal probability of sampling all individuals (Caughley 1977).

Long-term field studies of individually marked animals combined with appropriate statistical procedures has been suggested as the only viable means whereby to examine senescence in mammals (Gaillard *et al.* 1994). In view of the scarcity of such studies, the aim of the present study was to determine whether senescence is prevalent in southern elephant seal (*Mirounga leonina*) females at Marion Island, using 17 years of mark-recapture data. We also assessed longevity in the population. Senescence implies not only a decrease in adult survival, but also a decrease in reproductive rate or breeding probability with age (Promislow 1991). We therefore report on both these parameters in this study using longitudinal data derived from a large sample of marked individual southern elephant seal females. To our knowledge it is the first longitudinal study of senescence in a marine mammal, and of both components of senescence (survival and reproductive) in a mammal. The demographics of the southern elephant seal population at Marion Island have been detailed by Bester & Wilkinson (1994) and Pistorius *et al.* (1999a & b).

6.2 Methods

6.2.1 Data collection

A total of 1650 (average: 275 annually, range: 198-343) weaned female elephant seal pups were tagged in each of their hind flippers from 1983 to 1988 on Marion Island, using uniquely numbered, colour-coded Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom) (see Pistorius *et al.* 2000 for details). We searched for tagged seals at all the beaches utilised by elephant seals (32 along a 51.9 km coastline) on the island every seven days during the breeding season (mid-August to mid-November) and every 10 days during the moulting period (mid-November to mid-April) each year from 1983 to 2000, and every 10 days during the winter (June, July and August) since 1990. We recorded the tag number and colour combination of each tagged seal during these surveys.

6.2.2 Data analyses

Encounter-history matrices, which are required for capture-mark-recapture (CMR) analysis, were constructed for each cohort (1983-1988) from the year-round resight data of females in order to allow estimation of adult female survival. Multiple sightings in a year were treated as a single sighting. Seventeen years of recapture data was available for the 1983 cohort and 12 years for the 1988 cohort. Seals were assumed to age by one year on 15 October which is the peak breeding season haul-out date for adult females at Marion Island (Condy 1978; Bester & Wilkinson 1994). An encounter-history matrix was also created from the pooled resight data of females from the 1983 to 1988 cohorts, but limited to the breeding seasons. This was done for the purpose of estimating age-specific capture probabilities during the breeding seasons, which were used as indices of age-specific breeding probabilities (see Pistorius *et al.* 2001) of adult females. All females are recruited into the adult population by their 7th year (Wilkinson 1992; Pistorius *et al.* 2001) and the encounter-history matrix therefore consisted of recaptures of adult females 6 years and older that still carried tags as 5-year-olds. In addition, we constructed an encounter-history matrix from pooled breeding season resight data limited to the 1983-1986 cohorts so as to allow estimation of capture probabilities of females in their 14th and 15th year.

The software program MARK (G. White, University of Colorado), which is an application for the analysis of marked individuals, was used to obtain likelihood estimates of survival and capture probabilities using the above-mentioned matrices. The software program provides parameter estimates under the essential Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965), but also under several models that appear as special cases of this model (Lebreton *et al.* 1992).

The two fundamental parameters in these models are:

Φ = the survival probability for all animals between the ith and $(i + 1)$ th sample $(i = 1, \ldots, k - 1)$, and p = the capture probability for all animals in the ith sample $(i = 1, \ldots, k)$.

The first step in the mark-recapture analyses involved Goodness of Fit (GOF) tests of the CJS model (full time-dependent model) using the program RELEASE (Burnham *et al.* 1987) to validate the model assumptions (see Lebreton *et al.* 1992). As age dependence was assumed, and the different cohorts were treated separately, Test 3.Sm was retained (see Lebreton *et al.* 1992; Pistorius et al. 1999a).

Proper model selection, which is the primary issue in the analysis of CMR data (Anderson *et al.* 1994), was accomplished using the Akaike Information Criterion (AIC). AIC is a standard procedure for model selection in a CMR context, and it weighs the quality of fit (deviance) and the precision (via the number of parameters), so as to select the most parsimonious model that adequately describes the data (Lebreton *et al.* 1993; Anderson *et al.* 1994; Loison *et al.* 1994). When modelling adult female survival, it was used to select between the full-time dependent model and the constant-capture-probability model (assuming no year-to-year changes in capture probability), and between age dependent and constrained survival models for each cohort. The constraints placed on survival entailed reducing prime-age female survival to a single parameter and post 7th year survival (where senescence is expected to be prevalent (Promislow 1991)) to a single parameter in order to quantify a possible senescence effect in terms of reduced survival in southern elephant seals. We defined "prime-age" as the 4th to 7th year based on the certitude that females in these age groups contribute over 50% to the reproductive schedule of the population (Pistorius *et al.* 1999b). The model with the lowest AIC value was selected for each cohort. Using a Likelihood Ratio Test (LRT), an age dependent adult survival model was also compared to a model with constant survival from the 4th year onwards, in order to establish whether there were any age-effects on adult female survival for the respective cohorts. To determine whether any senescence effect after the 10th year of life was masked by comparatively high survival prior to this age (8th-10th year), we also constrained survival from the 11th year onwards. Sample sizes of seals this old were, however, small and we consequently pooled resights of the 1983-1986 cohorts prior to the analysis.

When modelling capture probabilities during the breeding seasons (pooled cohorts 1983-1988) we constrained capture probability over the 7th and 8th year, the 9th and 10th year and the 11th to 13th year and used these estimates if the model yielded a lower AIC value than the age dependent capture probability model. For the 1983-1986 cohorts, we constrained capture probability over the 7th to 12th year and the 13th to 15th year, to investigate any potential reduction in breeding probabilities of very old females.

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.

To investigate longevity, we totalled the number of females sighted at each age ≥10 years. These values were corrected for those individuals alive but not observed (using capture probabilities during moulting and breeding seasons over the same time period taken from Pistorius *et al.* (1999a)), and those not identified due to loss of both tags (tag retention rates taken from Pistorius *et al.* 2000). They were subsequently expressed as percentages of the numbers of females marked as pups.

6.3 Results

The CJS model fitted the year-round data for all the cohorts, except for the 1986 cohort, and the pooled year-round recapture data from the 1983-1986 cohorts (Table 9). The CJS model fitted the breeding season recapture data from the pooled 1983-1986 and 1983-1988 cohorts according to Tests 2 and 3 (Table 9).

In modelling survival, the constant capture probability model was more parsimonious than the full time-dependent model for three out of the six cohorts, and the constrained survival model more parsimonious for all the cohorts (Table 10). When comparing the constant adult female survival model with the age-dependent adult survival model, age-effects were evident in three of the six cohorts and not in the pooled 1983-1986 cohorts (Table 10).

In modelling capture probability, constant adult survival provided a more parsimonious model for the pooled 1983-1986 cohorts but not for the pooled 1983-1988 cohorts. In both cases constraints on capture probability resulted in improved models (Table 10).

After correction was made for tag loss, post 7th year survival diminished in two of the six cohorts relative to prime-age female survival (Table 12). On average there was, however, less than a 1% difference between prime-age and post 7th year survival, suggesting no senescence effect in terms of reduced survival in southern elephant seal females. When analysing the pooled 1983-1986 recapture data, prime-age female survival was 77.5% (S.E = 1.4%), 8th to 10th year survival 75.2% (S.E. = 2.9%), and 11th to 14th year survival 83.6% (S.E. = 4.2%). There was also no reduced survival manifested in the very old age classes and no reduction in capture probabilities of breeding females with age, suggesting the absence of reproductive senescence (Table 13).

Less than 5% of the female population live up to the age of 10 and about 0.5% reached age 17 (Table 14). Approximately 2.9% out of 1698 tagged male pups reached 10 years of age, around 0.5% out of 1402 tagged male pups reached 13 years of age, and not one of 469 tagged male pups survived to age 16.

Table 9. Goodness-of-fit tests of the Cormack-Jolly-Seber model by female southern elephant seal cohort for the Marion Island population.

Cohort	χ^2	*df*	*P*
Modelling survival probability			
1983	2.47	6	0.872
1984	12.87	6	0.103
1985	7.92	5	0.161
1986	10.22	4	0.037
1987	6.36	2	0.100
1988	16.72	9	0.108
1983-1986	22.67	5	<0.010
Modelling capture probability			
1983-1986	15.09	13	0.301
1983-1988	19.78	11	0.142

Table 10. Elimination of nonsignificant effects from the full CJS model in modelling survival and capture probability in southern elephant seal females at Marion Island: for each model the number of estimable parameters (np), the deviance (DEV), and the Akaike information criterion (AIC) are given.

Cohort	*Model*	*np*	*DEV*	*AIC*
Modelling survival probabilities				
1983	(1) (ϕ_t, p_t)	34	164.87	1139.21
	(2) (ϕ_t, p_c)	17	179.24	1116.02
	(3) $(\phi_{4-7, 8-}, p_c)$	6	189.74	**1103.50**
1984	(1) (ϕ_t, p_t)	31	234.48	1299.03
	(2) (ϕ_t, p_c)	17	257.42	1291.76
	(3) $(\phi_{4-7, 8-}, p_c)$	6	261.59	**1273.11**
1985	(1) (ϕ_t, p_t)	29	374.51	2134.08
	(2) (ϕ_t, p_c)	16	405.33	2137.54
	(3) $(\phi_{4-7, 8-}, p_t)$	20	381.85	**2122.39**
1986	(1) (ϕ_t, p_t)	27	283.32	1772.97
	(2) (ϕ_t, p_c)	15	297.51	1761.91
	(3) $(\phi_{4-7, 8-}, p_c)$	6	311.98	**1757.92**
1987	(1) (ϕ_t, p_t)	26	202.56	1837.43
	(2) (ϕ_t, p_c)	14	252.99	1862.74
	(3) $(\phi_{4-7, 8-}, p_t)$	18	216.42	**1834.46**
1988	(1) (ϕ_t, p_t)	22	244.86	1643.95
	(2) (ϕ_t, p_c)	13	294.06	1674.34
	(3) $(\phi_{4-7, 8-}, p_t)$	17	254.61	**1643.19**
1983-1986	(1) (ϕ_t, p_t)	27	794.70	6260.90
	(2) (ϕ_t, p_c)	15	818.84	6260.69
	(3) $(\phi_{4-7, 8-10, 11-13}, p_c)$	7	827.43	**6253.15**
Modelling capture probabilities				
1983-1986	(1) (ϕ_t, p_t)	17	120.75	1060.73
	(2) (ϕ_c, p_t)	10	132.44	1057.62
	(3) $(\phi_c, p_{7-12, 13-15})$	3	146.62	**1057.41**
1983-1988	(1) (ϕ_t, p_t)	13	76.81	1527.14
	(2) (ϕ_c, p_t)	8	103.33	1543.28
	(3) $(\phi_t, p_{7-8, 9-10, 11-13})$	10	83.11	**1526.92**

ϕ_t : Time/age-dependent survival rate; $\phi_{4-7, 8-}$: Constant survival during 4th to 7th year and 8th year onwards; $\phi_{4-7, 8-10, 11-13}$: Constant survival during 4th to 7th year, 8th to 10th year and 11th to 13th year

p_t: Time/age-dependent capture probability; $p_{7-8, 9-10, 11-13}$: Constant capture probability during 7th and 8th year, 9th and 10th year and 11th to 13th year; $p_{7-12, 13-15}$: Constant capture probability during 7th to 12th year and 13th to 15th year

Table 11. Testing the null hypothesis that adult female survival rates were constant across time, versus the alternative hypothesis that survival was age-dependent in southern elephant seal females.

Cohort	χ^2	*df*	*P*
1983	10.641	12	0.560
1984	4.224	12	0.979
1985	7.707	10	0.657
1986	17.443	10	0.065
1987	24.196	12	0.019
1988	12.162	6	0.059
1983-1986	10.976	11	0.445

Table 12. Survival rates of southern elephant seal females at Marion Island (corrected for tag loss).

Cohort	*4th-7th year*	*S.E.*	*8th year onwards*	*S.E.*
1983	0.738	0.035	0.754	0.060
1984	0.808	0.030	0.841	0.039
1985	0.744	0.028	0.745	0.047
1986	0.792	0.025	0.740	0.043
1987	0.747	0.044	0.750	0.049
1988	0.814	0.025	0.768	0.040

Table 13. Capture probabilities during the breeding seasons as indices of breeding probabilities of southern elephant seal females at Marion Island.

Cohorts	*Age*	*Capture probability*	*S.E.*
1983-1988	6 & 7	0.754	0.026
1983-1988	8 & 9	0.780	0.036
1983-1988	10-12	0.812	0.043
1983-1986	6-11	0.735	0.024
1983-1986	12-14	0.822	0.073

Table 14. Longevity in southern elephant seal females at Marion Island (individuals alive at each age represent those sighted at that age divided by 0.75 to account for those not sighted with additional tag loss compensation).

Age	*Individuals*	*Sample tagged*	*Probability of surviving up to age*
10	79	1650	0.048
11	67	1650	0.041
12	56	1650	0.033
13	37	1365	0.027
14	18	1053	0.017
15	9	775	0.012
16	5	432	0.012
17	1	198	0.005

6.4 Discussion

A recent discussion on the methodological problems associated with obtaining reliable evidence supporting or rejecting senescence in large mammal populations stressed the importance of long-term monitoring of marked individuals (Gaillard *et al.* 1994). Using marked individuals from several rather than a single cohort was also strongly recommended, so as to avoid the confounding effects of annual variation in survival. This study is therefore particularly relevant to an understanding of senescence in mammals and eminently so in marine mammals.

We found no evidence for a senescence effect in terms of either reduced survival or diminishing breeding probabilities with age in southern elephant seal females. Mortality over the various age classes therefore resulted in no individuals surviving to the age where physiological decline would become a mortality agent or result in failure to breed. Very few previous longitudinal studies have reported on senescence due to the inherent difficulties associated with obtaining sufficient data to permit reliable estimation of demographic parameters of old individuals. The actuality of senescence (in terms of reduced survival) was for the first time statistically demonstrated in two populations of roe deer (*Capreolus careolus*) that were monitored for 11 and 13 years respectively (Gaillard *et al.* 1993). Jorgenson *et al.* (1997) also concluded that senescence was evident for both sexes in two separate populations of bighorn sheep (*Ovis canadensis*) that were monitored for 13 and 20 years respectively. In both these studies, increasing tooth wear with age was suspected to contribute to senescence. In a long-term study of female chamois (*Rupicapra rupicapra*), Loison *et al.* (1994) found no evidence of senescence.

Longitudinal studies of ungulates that revealed evidence of senescence (Gaillard *et al.* 1993; Jorgenson *et al.* 1997) dealt with populations in which adults were unconstrained by food limitation. In bighorn sheep density dependence was only evident in yearlings, with population limitation depending upon changes in either the production or the survival of lambs (Jorgenson *et al.* 1997), and in roe deer, juvenile rather than adult survival was very sensitive to external influences (Gaillard *et al.* 1993). The southern elephant seal population at Marion Island, on the other hand, appears to be a food limited population in which ultimate regulation takes place through changes in adult female survival, with juvenile survival being largely unaffected (Pistorius *et al.* 1999a). This demographic dichotomy, evidenced by the high adult survival rates of the two ungulate populations relative to the southern elephant seal population (prime-age female survival for bighorn sheep 94-95%, for roe deer 93-97% and for southern elephant seals 77%), could ultimately explain the prevalence and absence of senescence in the ungulate and southern elephant seal populations respectively. In populations with very high adult survival rates, one would expect survivors at the age where the effects of senescence become realised. It therefore follows that the occurrence of senescence in natural populations may pre-eminently be determined by the means of population regulation and the population component/s that are targeted by the regulating agent/s.

Female survival over the 11th to 14th year age bracket was considerably higher than younger adult female survival (6-8% higher). Increasing survival rates with age in adults have been observed in few other large mammals and several hypotheses have been proposed to explain this phenomenon (Boer 1988; Promislow 1991). Promislow (1991) contended that short-term selection might lead to decreasing susceptibility to the impetus of mortality with age. It is reasonable to assume that better adapted seals in a cohort tend to survive through adulthood. The older individuals may therefore be of better than average quality compared with the cohort into which they were born, which would subsequently result in a relative increase in survival over the older age groups. This argument does, however, imply that any senescence effect, irrespective of the species involved, may be masked by the increasing quality of individuals remaining at the stage where senescence is expected to be prevalent. A future prerogative in the study of senescence should be to study whether long-lived individuals are in reality a random sample of the population and to identify individual traits that affect longevity (Jorgenson *et al.* 1997). A second explanation for the increase in survival late in life could be that survival rates increase as a result of learning and experience. Older individuals may, for example, be more efficient foragers, or more adept at evading predators (Boer 1988).

As in the present study, Promislow (1991) mostly measured senescence from the onset of sexual maturity. He noted that there was often a peak in mortality immediately following primiparity. This could potentially have biased the comparison with older age groups when searching for evidence of senescence, and in these cases he measured senescence from the age class following this peak. Except for females primiparous at a late age, southern elephant seal females at Marion Island show no such an increase in mortality (Chapter 8), thereby avoiding a similar potential bias. Promislow (1991) found that in some populations, senescence only became apparent very late in life (up to twice the age of maturity), in contrast to the present study where there was no manifestation of senescence even well beyond this stage.

In modelling survival, the 1986 cohort and the pooled recapture data from the 1983-1986 cohorts did not fit the CJS model satisfactorily. We suspect that deviation from the CJS model was due to heterogeneity in capture probability during the moulting periods. Despite the fact that elephant seal females display high levels of site fidelity during the breeding seasons (Hindell & Little 1987; Hofmeyr 2001), they are known to frequently haul out on non-natal localities (e.g., other islands) to moult (Bester 1989). This tendency is not uniform among individuals (Bester 1989; Hofmeyr 2001), thereby resulting in heterogeneity in capture probability at this time. When comparing survival estimates from the pooled data collected during the breeding seasons for the 1983-1986 cohorts (good fit according to Tests 2 and 3), they were similar to those derived from the year-round resight data (<1.2% difference) which did not fit the CJS model. We therefore assume that deviation from the CJS model resulted in minimal bias in the survival estimates.

This study of senescence was limited to female southern elephant seals as a result of the confounding effect that mortality resulting from aggressive male to male interactions, associated with the extremely polygynous existence of elephant seals, may have had on senescence. Belligerence is not uniform over the adult male age classes, and is expected to increase with age since some males only attain beachmaster status very late in life (pers. obs.). This therefore makes it impossible to separate mortality attributable to the degenerative processes resulting from ageing (i.e., senescence) from mortality resulting from aggressive behaviour. Adult male elephant seals also have significantly higher mortality rates than females (Pistorius *et al.* 1999a), and sample sizes of old marked males are consequently substantially lower than that for females (present study), making them less suitable for a study of senescence.

In this study we used capture probability of females during the breeding season as an index of breeding probability, similar to a previous study by Pistorius *et al.* (2001). This methodology is justified as a thorough and rigid recapture program has been in place since the commencement of the marking program. We assumed that if reproductive senescence was a reality in elephant seal females, that this would have been manifested in failure to breed on occasions, rather than abrupt termination of breeding. If abrupt termination of breeding were the case, the models used would have interpreted breeding cessation as mortality since only breeding season recaptures were included. As virtually all elephant seal females that haul out during the breeding season do so to give birth (Huber *et al.* 1991; Wilkinson 1992), we consider the observed constant capture probability with age to be a true reflection of the breeding probability. Furthermore, adult female elephant seals at Macquarie Island have been recorded to give birth up to 22 years of age (Hindell & Little 1988), the approximate limit for longevity of southern elephant seals at South Georgia (McCann 1985). We therefore suggest that female southern elephant seals continue to breed until shortly before death. This is in contrast with the otariids *Callorhinus ursinus* and *Arctocephalus tropicalis* where a post-reproductive class of females exists (*vide* York & Hartley 1981; Bester 1995), but not in *A. gazella* where there was no evidence of a decline in pregnancy rates of older females (Payne 1977). Reproductive failures commenced as early as 12 years of age in *A. tropicalis* (Bester 1987), increasing progressively towards at least 23 years of age, the usual longevity of fur seal females (Wickens 1993). The cross-sectional nature of the *A. tropicalis* data, however, precluded comment on whether or not reproductive failures were soon followed by death (and therefore whether senescent mortality was prevalent).

In the present study less than 1% of 1698 marked male pups survived up to age 12, with a maximum longevity of 15 years. About 1% of females survived up to age 15, with longevity of 17 years being recorded in a single female. Through the counting of annual layers in tooth cementum or dentine, longevity of southern elephant seals at South Georgia was reported to be 20 and 19 years for males and females respectively (McCann 1985) and two 22-year-old females were recorded breeding at Macquarie Island (Hindell & Little 1988). At Marion Island (at least) a very small proportion (if any) survive up to these ages and we caution against unjustified use of such high estimates in life table analyses and demographic extrapolations of southern elephant seal populations.

CHAPTER 7 SURVIVAL OF PUBESCENT SOUTHERN ELEPHANT SEAL MALES: A TEST OF THE FOOD LIMITATION HYPOTHESIS AND ASSESSMENT OF ENVIRONMENTAL FLUCTUATIONS

7.1 Introduction

The southern elephant seal population at Marion Island has been declining at least since the 1950s and it is now at approximately 10% of its size in 1951 (Bester & Wilkinson 1994; Laws 1994; Pistorius *et al.* 1999b). The population declined by 37.2% from some 2120 individuals in 1986 to 1330 individuals in 1994 at a 5.8% annual rate of change, which was linear over the period (Pistorius *et al.* 1999b). A great deal of concern and speculation have been associated with this decline, particularly since it has occurred on a large scale involving most Indian and Pacific Ocean southern elephant seal populations (Hindell & Burton 1987; Guinet *et al.* 1992; Bester & Wilkinson 1994; Hindell *et al.* 1994; Pistorius *et al.* 1999b). The decline now appears to be halted over most of the Kerguelen stock of elephant seals (Guinet *et al.* 1999; Pistorius *et al.* 1999b), and the Heard Island population appears to be increasing (Slip & Burton 1999). Proposed reasons for the decline have been varied with Hindell *et al.* (1994) providing a thorough review and account of possible causes for the declines. As an intrinsic factor, density-dependent pup mortality was proposed, which has subsequently been dismissed as a causative factor, at least at Marion Island (Chapter 3). Predation by killer whales has also been suggested as a possible factor. These predators also target juvenile southern elephant seals (Condy *et al.* 1978). This population component has been characterised by reasonably high and consistent survival at Marion Island (Chapter 4) thereby suggesting that predation has had a small impact on the population. Food availability was also suggested to be responsible for the declines as follows: The first notion, interspecific competition, seems unlikely due to poor adult female survival being singled out as the main reason for the population decline at Marion Island (Pistorius *et al.* 1999a). These animals forage on deep-dwelling benthic and pelagic prey, which are generally unavailable to other mammal or bird species (Hindell *et al.* 1991; Jonker & Bester 1998), although ziphiid odontocete whales such as the southern bottlenose whale (*Hyperoodon planifrons*) have been identified as potential competitors (Slip 1995). The second, referred to as the "overshoot" hypothesis, proposes that the decline was a direct consequence of the heavy exploitation of elephant seals during the eighteenth and early nineteenth century. Prey species were thereby allowed to show a drastic increase, which when sealing activities were terminated in the early nineteenth century, formed an abundant resource. Elephant seals responded numerically and the following decline is proposed to be a result of the subsequent overexploitation of the food resource and a decrease towards equilibrium (Hindell *et al.* 1994). The Marion Island population stabilised at approximately 1300 individuals in 1994, and the population has been maintained at this level ever since (Chapter 5). The third food related hypothesis suggests that the declines were a consequence of changes in the ocean environment that impacted on the prey resources of elephant seals, with El Niño Southern Oscillation (ENSO) events possibly having contributed to these changes (Hindell *et al.* 1994).

In animals exhibiting sexual dimorphism, the larger morph is generally the most susceptible to nutritional stress and hence more prone to starvation during periods of food shortage (Toigo *et al.* 1997; Pistorius *et al.* 1999a). Southern elephant seals are the most sexually dimorphic mammals, with sexual dimorphism becoming pronounced after 12 months of age (Bell *et al.* 1997), and males of this species have higher mortality rates than females as a result of the relative increased energetic requirements (see Pistorius *et al.* 1999a). In addition, males undergo a spurt of secondary growth in their 4th to 6th year during which food requirements are greatly increased (Ling & Bryden 1981; Laws 1984). In order to test whether food limitation regulates, and hence has been responsible for the decline of the southern elephant seal population at Marion Island, we make use of long-term monitoring data to compare survival estimates from this population component with conceivably high energetic demands during (1986-1993) and after (1994-1998) the population decline. Under the food limitation hypothesis we would expect a significant increase in survival of males undergoing a secondary growth spurt concurrent with the stabilisation of the population. In addition, we search for a temporal pattern in survival of these animals. We consequently investigate the potential that the population has been indirectly responding to physical oceanographic processes by correlating survival with ENSO events.

7.2 Methods

7.2.1 Data collection

A total of 3270 (average: 252 annually, range: 198-343) male elephant seal pups were double tagged in their hind flippers after weaning from 1983 to 1995 on Marion Island, using uniquely numbered, colour-coded (to allow subsequent age determination) Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom) (for more detail see Pistorius *et al.* 2000). For the period 1983-2000 all the beaches (32 along a 51.9-km coastline) were searched for tagged seals every 7 to 10 days during the entire year except for winter months (June, July and August) prior to 1990 when no resights were made. For each tagged seal that was resighted, attempts were made to record the tag number and colour combination, the number of tags remaining (one or two) and date of sighting.

7.2.2 Data analyses

Encounter-history matrices, which are required for capture-mark-recapture analyses, were constructed from the resight data of males from the 1983 to 1995 cohorts, treating multiple sightings at a particular age as a single sighting. Seals were assumed to age by one year on 15 October which is the peak haul-out date for adult females giving birth at Marion Island (Condy 1978; Bester & Wilkinson 1994). The software program MARK (G. White, University of Colorado), which is an application for the analysis of encounter-history matrices of marked individuals, was used to obtain likelihood estimates of survival and capture probabilities of males in their 4th, 5th and 6th year (hence forth referred to as pubescent males). The software program provides parameter estimates under the essential Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965), but also under several models that appear as special cases of this model (Lebreton *et al.* 1992). As it was impossible to distinguish mortality from permanent emigration in our study, we refer to apparent rather than absolute survival.

The two fundamental parameters in these models are: Φ = the survival probability for all animals between the *i*th and (*i* + 1)th encounter occasion ($i = 1, \ldots, k-1$), and p = the capture probability for all animals in the *i*th encounter occasion ($i = 1, \ldots, k$).

The first step in the mark-recapture analysis involved Goodness of Fit (GOF) tests of the CJS model (full time-dependent model) using the program RELEASE (Burnham *et al.* 1987) to check whether the assumptions pertaining to the model were met (see Lebreton *et al.* 1992). As age dependence was assumed, and the different cohorts were treated separately, Test 3.Sm was retained (see Lebreton *et al.* 1992; Pistorius *et al.* 1999a). This test was performed recently for the 1983-1992 cohorts (see Pistorius *et al.* 1999a) and in this study we limit the GOF test to the 1993-1995 cohorts.

Proper model selection, which is the primary issue in the analysis of capture-mark-recapture (CMR) data (Anderson *et al.* 1994), was accomplished using the Akaike Information Criterion (AIC). AIC is a standard procedure for model selection in a CMR context, and it weighs the quality of fit (deviance) and the precision (via the number of parameters), so as to select the most parsimonious model that adequately describes the data (Lebreton *et al.* 1993; Anderson *et al.* 1994; Loison *et al.* 1994). It was used to select between the full time-dependent model and the constant-capture-probability model (assuming no year-to-year changes in capture probability) for each cohort. The model with the lowest AIC value was selected for each cohort. A likelihood-ratio-test was used to test for age-dependence in pubescent male survival for each cohort (comparing a model with pubescent survival age-dependent with a model in which pubescent survival was constant over age; see Lebreton *et al.* 1992) after which constraints were placed on survival in search of a more parsimonious model. These constraints involved maintaining survival over the first three years, over the 4th to 6th year (for cohorts with no age-dependence in pubescent survival) and from the 7th year onwards constant, and if this reduced the AIC value the model was selected. For the 1988 and 1989 cohorts 4th to 6th year survival was separated according to population status at the time (see below).

Survival of pubescent males during the population decline (1986-1993) was averaged over the period and compared to their survival after the decline (1994-1999) in order to quantify its response to the population stabilisation.

I also constructed a single capture history matrix from recapture data from all the cohorts to test the hypothesis that there was a significant increase in pubescent survival concurrent with the stabilisation of the population. A likelihood-ratio-test was used for this purpose and a model with pubescent survival constant over time was compared with a model in which pubescent survival was both constant during the population decline and after the decline.

In order to investigate temporal changes in pubescent male survival, we modelled age-specific pubescent survival (separate estimates for the 4th, 5th, and 6th year) for each cohort. We subsequently averaged year-specific pubescent survival for the period 1987 to 1999 and these estimates were plotted on a graph. We refer to the post birth-date (see above) calendar years, but it should be born in mind that these represent years between elephant seal birth dates (e.g., 1987 survival describes survival for the period October 1986 to October 1987).

Cumulative age-specific tag retention rates, estimated from double-tagged individuals (Pistorius *et al.* 2000), were used to adjust all survival estimates to compensate for tag loss.

7.3 Results

The CJS model fitted the data for the 1993 cohort ($\chi^2 = 3.33$, df = 3, $p = 0.34$), but not for the 1994 and 1995 cohorts ($p < 0.01$) suggesting violation of the underlying assumptions of the model. In addition, the 1983, 1985, 1986, 1987 and 1990 cohorts showed departures from the CJS model (see Pistorius *et al.* 1999a).

Only three cohorts (1986, 1989, and 1995) showed evidence for age-dependence in pubescent survival (1983: $\chi^2 = 0.26$, df = 2, $p = 0.88$; 1984: $\chi^2 = 1.33$, df = 2, $p = 0.51$; 1985: $\chi^2 = 4.92$, df = 2, $p = 0.10$; 1986: $\chi^2 = 5.13$, df = 1, $p = 0.02$; 1987: $\chi^2 = 3.96$, df = 2, $p = 0.14$; 1988: $\chi^2 = 0.92$, df = 2, $p = 0.63$; 1989: $\chi^2 = 9.25$, df = 2, $p = 0.01$; 1990: $\chi^2 = 2.08$, df = 2, $p = 0.35$; 1991: $\chi^2 = 2.39$, df = 2, $p = 0.30$; 1992: $\chi^2 = 2.04$, df = 2, $p = 0.36$; 1993: $\chi^2 = 1.94$, df = 2, $p = 0.379$; 1994: $\chi^2 = 5.55$, df = 1, $p = 0.02$). For the majority of cohorts the constant capture probability model proved to be more parsimonious than the full time-dependent model, and constraints on survival were justified for most cohorts (Table 15).

Fig. 6. Survival of pubescent males (4th - 6th year) at Marion Island

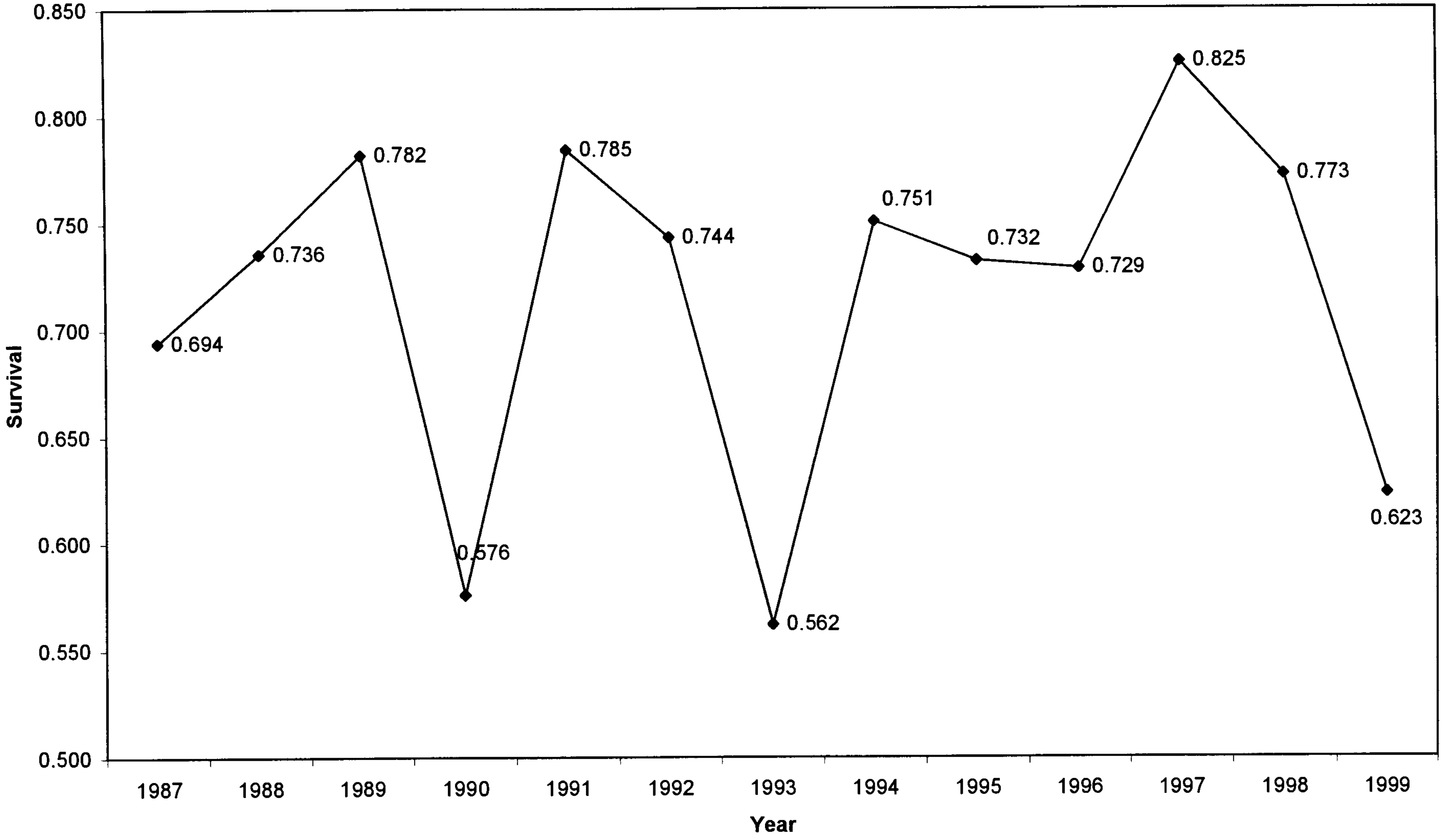

Table 15. Elimination of nonsignificant effects from the full CJS model in modelling 4th, 5th and 6th year male survival in southern elephant seals from Marion Island: for each model the number of estimable parameters (np), the deviance (DEV), and the Akaike information criterion (AIC) are given

Cohort	*Model*	*np*	*DEV*	*AIC*
1983	(1) (ϕ_{t}, p_{t})	28	192.35	1136.14
	(2) (ϕ_{t}, p_{c})	17	206.51	1126.10
	(3) $(\phi_{(1\text{-}3,4\text{-}6,7\text{-})}, p_{c})$	4	218.57	**1110.96**
1984	(1) (ϕ_{t}, p_{t})	29	131.82	1170.94
	(2) (ϕ_{t}, p_{c})	16	152.41	1163.18
	(3) $(\phi_{(1\text{-}3,\ 4\text{-}6,7\text{-})}, p_{c})$	4	161.21	**1147.02**
1985	(1) (ϕ_{t}, p_{t})	25	223.67	1816.51
	(2) (ϕ_{t}, p_{c})	15	241.00	1812.85
	(3) $(\phi_{(1\text{-}3,\ 4\text{-}6,7\text{-})}, p_{c})$	4	256.28	**1805.60**
1986	(1) (ϕ_{t}, p_{t})	22	149.42	1322.99
	(2) (ϕ_{t}, p_{c})	14	167.18	1323.80
	(3) $(\phi_{(1\text{-}3,\ 4,5,6,7\text{-})}, p_{t})$	18	168.42	1329.23
	(4) $(\phi_{(1,2,3,\ 4,5,6,7\text{-})}, p_{t})$	20	151.80	**1321.09**
1987	(1) (ϕ_{t}, p_{t})	22	179.22	1430.71
	(2) (ϕ_{t}, p_{c})	13	184.70	1417.22
	(3) $(\phi_{(1\text{-}3,\ 4\text{-}6,7\text{-})}, p_{c})$	4	213.45	1427.51
	(4) $(\phi_{(1,2,3,\ 4\text{-}6,7\text{-})}, p_{c})$	6	195.83	**1413.94**
1988	(1) (ϕ_{t}, p_{t})	20	195.64	1545.25
	(2) (ϕ_{t}, p_{c})	12	205.18	1538.06
	(3) $(\phi_{(1\text{-}3,\ 4\text{-}5,6,7\text{-})}, p_{c})$	5	224.64	1543.16
	(4) $(\phi_{(1,2,3,\ 4\text{-}5,\ 6,7\text{-})}, p_{c})$	7	217.33	**1537.89**
1989	(1) (ϕ_{t}, p_{t})	19	156.98	1157.05
	(2) (ϕ_{t}, p_{c})	11	161.16	1144.30
	(3) $(\phi_{(1\text{-}3,\ 4,5,6,7\text{-})}, p_{c})$	6	197.06	1167.83
	(4) $(\phi_{(1,2,3,4,5,6,7\text{-})}, p_{c})$	8	162.18	**1139.10**
1990	(1) (ϕ_{t}, p_{t})	17	187.39	1217.73
	(2) (ϕ_{t}, p_{c})	10	201.29	1216.93
	(3) $(\phi_{(1\text{-}3,\ 4\text{-}6,7\text{-})}, p_{c})$	4	211.63	**1214.96**
1991	(1) (ϕ_{t}, p_{t})	15	156.93	1133.98

	(2) (ϕ_t, p_c)	9	169.89	1134.41
	(3) $(\phi_{(1\text{-}3,\ 4\text{-}6,7\text{-})}, p_t)$	11	168.60	1137.27
	(4) $(\phi_{(1,2,3,\ 4\text{-}6,7\text{-})}, p_t)$	13	159.32	**1132.16**
1992	(1) (ϕ_t, p_t)	13	120.36	945.48
	(2) (ϕ_t, p_c)	8	123.37	938.02
	(3) $(\phi_{(1\text{-}3,\ 4\text{-}6,7)}, p_c)$	4	152.79	959.23
	(4) $(\phi_{(1,2,3,\ 4\text{-}6,7)}, p_c)$	6	125.40	**935.93**
1993	(1) (ϕ_t, p_t)	11	142.07	1163.72
	(2) (ϕ_t, p_c)	7	145.74	1159.11
	(3) $(\phi_{(1\text{-}3,\ 4\text{-}6)}, p_c)$	3	154.23	1159.44
	(4) $(\phi_{(1,2,3,\ 4\text{-}6)}, p_c)$	5	147.69	**1156.96**
1994	(1) (ϕ_t, p_t)	9	71.63	910.67
	(2) (ϕ_t, p_c)	6	73.98	**906.81**
	(3) $(\phi_{(1\text{-}3,\ 4,5)}, p_c)$	4	92.71	919.41
	(4) $(\phi_{(1,2,3,\ 4,5)}, p_c)$	5	79.53	908.27
1995	(1) (ϕ_t, p_t)	7	70.61	830.69
	(2) (ϕ_t, p_c)	5	70.91	**826.86**
	(3) $(\phi_{(1\text{-}3,\ 4)}, p_c)$	3	100.71	852.58

ϕ_t : Time/age-dependent survival rate; $\phi_{(1\text{-}3,\ 4\text{-}6,\ 7\text{-})}$: Survival constant over the first three years, 4th to 6th year and 7th year onwards; $\phi_{(1,2,3,\ 4\text{-}6,\ 7\text{-})}$: Survival time/age dependent during the first three years, constant over the 4th to 6th year and 7th year onwards; p_t: Time/age-dependent capture probability; p_c: Constant capture probability

Table 16. Survival rates of sub-adult/pubescent males from Marion Island (corrected for tag loss)

Cohort	*Age*	*Year*	ϕ	*S.E.*(ϕ)	*p*	*S.E. (p)*
1983	3-5	1987-1989	0.726	0.043	0.637	0.027
1984	3-5	1988-1990	0.725	0.048	0.649	0.030
1985	3-5	1989-1991	0.708	0.033	0.689	0.022
1986	3	1990	0.564	0.066	0.771	0.071
	4	1991	0.864	0.089	0.750	0.088
	5	1992	0.658	0.096	0.825	0.071
1987	3-5	1991-1993	0.665	0.038	0.738	0.024
1988	3-4	1992-1993	0.706	0.042	0.658	0.034
	5	1994	0.743	0.022	0.658	0.034
1989	3	1993	0.431	0.063	0.710	0.026
	4	1994	0.693	0.097	0.710	0.026
	5	1995	0.821	0.110	0.710	0.026
1990	3-5	1994-1996	0.718	0.038	0.723	0.028
1991	3-5	1995-1997	0.749	0.039	?	?
1992	3-5	1996-1998	0.722	0.043	0.758	0.028
1993	3-5	1997-1999	0.824	0.036	0.713	0.026
1994	3	1998	0.767	0.074	0.763	0.028
	4	1999	0.466	0.088	0.763	0.028
1995	3	1999	0.667	0.081	0.763	0.030

On average (using separate cohort models), pubescent survival during the population decline (1987-1993) was 68.9% and during the stable phase it was 73.3% (Table 16). There was therefore a 4.4% increase in survival of this population component associated with the stabilisation of the population. From a combined model (incorporating recapture data from all cohorts), we estimated an annual pubescent survival probability of 66.9% (S.E. = 1.6%) during the population decline which increased to 73.2% (S.E. = 1.8%) after the decline. According to this model there was therefore a 6.3% increase in survival, with this difference between the two periods being significant ($\chi^2 = 6.85$, df = 1, p = 0.009).

Temporal variation in pubescent male survival was evident over the study period, with survival ranging from 56.2% to 82.5% (mean = 71.6%). A distinct three-year cycle was apparent, with survival in 1987, 1990, 1993 and 1999 on average being approximately 15% (range: 6.8%-20%) lower than for the other years. The 1996 estimate was the lowest of the remaining estimates, but only slightly so.

7.4 Discussion

A significant increase in pubescent male survival of between 4.4% and 6.3% was associated with the halt in the decline of the southern elephant seal population at Marion Island. This lends support to the food limitation hypothesis and together with results from Pistorius *et al.* (1999a) I argue that the population decline was driven by food limitation. The survival of adult females, particularly that of recently sexually mature females, has also increased concurrently with the stabilising of the Marion Island population (Chapter 5), while juvenile survival remained unaffected (Chapter 4). These females are likely, together with pubescent males, to have relatively high energetic demands as a response to increased physiological stress and energetic demands imposed by gestation and the postpartum lactation period (Bester & Wilkinson 1994; Hastings *et al.* 1999). This is expected to be exacerbated by the phase of continuing body growth which would also increase energetic demands relative to the older females (Laws 1953; Reiter *et al.* 1981; Reiter & Le Boeuf 1991; Pistorius *et al.* 1999a). The increases in survival of this population component, as well as in pubescent males, are both in support of the food limitation hypothesis. Relative to these individuals, juveniles are expected to have relatively low absolute energy requirements and hence the stability in their survival.

When evaluating the data in terms of meeting the underlying assumptions of the CJS model, the majority of cohorts failed to pass the GOF test, suggesting heterogeneity in survival and/or capture probability within groups of individuals last released on the same sampling occasion. We suspect survival to be homogenous amongst individuals, although size, and therefore condition, at weaning clearly 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 probably due to various levels of philopatry (Hofmeyr 2001). To reduce the extent of this heterogeneity we analysed recapture data from each cohort separately (to avoid heterogeneity due to intrinsic factors and differences in the clarity of the numbers on the tags among cohorts). To test for a significant difference in survival over the two periods we used recapture data from all the cohorts in a single model. This model showed a relatively poor fit to the data and estimates from the single cohort models are likely to be more realistic. Heterogeneity among individuals with different capture histories, and departures from the CJS model in general, does not appear to affect point estimates of survival (Carothers 1979), although it may cause underestimation of standard errors of survival estimates (Burnham *et al.* 1987).

Southern elephant seals at Marion Island are near the top of the trophic pyramid and their response to environmental factors therefore integrates perturbations lower in the food web. Pubescent male survival showed significant fluctuations throughout the study period. When accepting the food limitation hypothesis, this implies marked fluctuations in the southern Indian Ocean environment, which in turn impacts on the food resources of the southern elephant seal population. The foraging range of southern elephant seal males from Marion Island has been documented and it does indeed cover a large part of the southern Indian Ocean (Malherbe 1998; Stewart & Bester, unpublished data). These environmental fluctuations are therefore likely to be operative on a large scale rather than being confined to the Marion Island region of the southern Indian Ocean.

Pubescent male survival demonstrated a distinct three-year cycle with particularly low survival in 1987, 1990, 1993 and 1999. A similar pattern was evident for young adult females (4th and 5th year) with high energetic demands (see above) and for females immediately prior to the age of potential primiparity over the period 1986 through 1996 (over the three age categories survival for 1987 was 11.3%, for 1990, 3.5% and for 1993, 10.2% lower than the average for the study period; Pistorius *et al.* 1999b). We speculate that some large-scale environmental process has been responsible for this cyclical pattern and it is conceivable that it has had a strong bearing on the decline of a number of elephant seal populations over the past several decades.

The phenomenon known as El Niño is generally regarded as the world's largest climate system having an impact on fisheries and marine life, as well as climatic conditions around the globe. Its effects on northern hemisphere pinnipeds have been frequently reported (Trillmich & Limberger 1985; Trillmich 1991; DeLong & Antonelis 1991), but less so for the southern hemisphere. It is thought to extend all the way south to Antarctica where it possibly impacts on pup production in the Weddell seal population, and this may be a result of changes in the fish populations caused by shifts in ocean currents (Testa *et al.* 1991 & Bester & Odendaal 2000). Similarly, pup production in Antarctic fur seals (*Arctocephalus gazella*) at subantarctic Possession Island (Iles Crozet) have been reported to be significantly lower the year after ENSO events (Guinet *et al.* 1994), whereas weaning mass of southern elephant seals at King George Island were lower during El Niño years (Vergani *et al.* 2001).

El Niño events occurred in 1986-1987, 1992, 1995 and 1997-1998. A three-year cycle can be evoked from these El Niño years by considering 1986, 1992, 1995 and 1998. These years correlate with male survival in the present study, all of them directly preceding low pubescent male survival years. A strong La Niña event (see Philander 1990) occurred in 1988-1989, which may have been influential in the relatively low survival estimate of 1990. There is, however, a one year lag in response which demands explanation.

The extensive fluctuations in pubescent survival over time have had implications for deriving and comparing survival rates over the two time periods. In the present study there are four years in which survival was particularly low (1987, 1990, 1993 and 1999; Fig. 1). The number of these low estimates included in each time period is anticipated to have had a major influence on the comparison of survival over the two time periods. If a three-year cycle is accepted, then we incorporated three lower survival estimates in the declining phase and only two in the stable phase which would have positively biased the survival estimate over the stable period in terms of the comparison. When excluding the low estimate of 1993 from the declining phase, we did, however, still find a 2% increase in survival with the stabilisation of the population suggesting that the increase in survival in the latter period was real.

The dearth in information on the southern ocean ecosystem greatly hampers the interpretation of our results. It is evident from this study that the survival of elephant seal males with relatively high energetic demands increased in recent years and this appears to be associated with the stabilisation of the population as a response to a relative increase in food abundance. The major fluctuation in survival of these animals is a likely response to a similar fluctuation in their food resources, particularly cephalopods, as they form a major part of the diet of southern elephant seals (Laws 1977; Slip 1995). ENSO may be tied in with these fluctuations but we have not found a causal link between these events and changes in survival of elephant seals or that of their prey.

CHAPTER 8 THE CONSEQUENCES OF EARLY PRIMIPARITY IN SOUTHERN ELEPHANT SEALS: A TEST OF A LIFE HISTORY THEORY PREDICTION IN A CAPITAL BREEDER

8.1 Introduction

The distribution of life-history traits in a population and factors responsible for this distribution form an important issue in population ecology as they are likely to influence both the fluctuations in numbers and the evolutionary dynamics within the population (Lande 1982; Saether & Heim 1993). The timing of sexual maturity in mammals is often correlated with life expectancy, even after accounting for differences in body size (Harvey & Zammuto 1985). Nonetheless, age of first reproduction varies substantially within and among populations of most large mammals (e.g. Clutton-Brock *et al.* 1988; Skogland 1989; Saether & Heim 1993; Bester & Wilkinson 1994; Pistorius *et al.* 2001). The causes for that variability have been variously suggested, though there is no consensus yet (cf. Reiter & Le Boeuf 1991; Gaillard *et al.* 1992; Jorgenson *et al.* 1993; Saether & Heim 1993).

According to life history theory, natural selection is expected to favour a reproductive strategy that takes into account the average chances of successful reproduction at any age and the consequences of breeding for subsequent survival and reproduction (Gadgil & Bossert 1970; Jorgenson *et al.* 1993). When the chances of survival are low animals should, for example, breed as early as possible (Harvey & Zammuto 1985). Deferred reproduction is accordingly a result of a trade-off between current reproductive effort and subsequent reproduction, growth, and/or survival (Reiter *et al.* 1981; Reiter & Le Boeuf 1991; Boyd *et al.* 1995). Consequently, conflicting selective pressures will act on a young seasonally breeding female in average body condition. If she breeds, her survival and body growth may be compromised, but if breeding is delayed her total reproductive success may be lowered and she may die before the next breeding season.

In northern elephant seals and Antarctic fur seals, females that give birth early in life evidently have lower future reproductive success and poorer survival than those that give birth for the first time later in life (e.g., Huber 1987; Lunn *et al.* 1994; Reiter & Le Boeuf 1991; Sydeman & Nur 1994). Similar reductions in these vital rates associated with early breeding have been reported for several ungulate species (Clutton-Brock 1983; Miura *et al.* 1987). In contrast, bighorn ewes (*Ovis canadensis*) and bison (*Bison bison*) females that breed at an early age of primiparity have been shown to have the same or better survival and reproductive success than females that breed at an older age (Festa-Bianchet 1989; Green & Rothstein 1991).

Here we document the fitness correlates of variation in age of first reproduction in southern elephant seal females at Marion Island in terms of the patterns of later survival and breeding success using recapture data that was collected during the period 1986 to 1999 from marked females. According to life history theory, we would expect reduced future survival and/or breeding probabilities in early breeders relative to females that delay the onset of reproduction, so as to equal out lifetime fitness (Gadgil & Bossert 1970). On the other hand, if mass or body size is the fundamental criterion affecting age of first breeding (Laws 1956b; Reimers *et al.* 1983; Jorgenson *et al.* 1993; Boyd 2000), then the above-mentioned age-specific estimates of females breeding for the first time at the various ages is expected to be similar, with early breeders gaining a competitive advantage in terms of gene investment.

Primiparous southern elephant seal females range in age from three to six years, a time when active growth is still taking place, and adult females start hauling out onto land to breed in early September and peak in numbers in mid-October (Wilkinson 1992; Bester & Wilkinson 1994). Females rely entirely upon stored energy reserves to feed their offspring to weaning and are extreme examples of capital breeders (Jonsson 1997; Boyd 2000). They give birth to a single pup about a week after hauling out, wean the pup in three weeks during which a massive transfer of energy takes place involving a 35% loss in the mother's weight (Fedak *et al.* 1996), and then depart to sea again (Condy 1979; Wilkinson 1992). Once the adult reproductive pattern is reached breeding takes place annually, although intermittent breeding of females primiparous at a young age, as in northern elephant seals, is conceivable (Huber 1987; Wilkinson 1992).

8.2 Methods

8.2.1 Data collection

We marked 2166 (average: 271 annually, range: 198-343) female elephant seal pups with uniquely numbered, colour-coded Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom) in each of their hind flippers shortly after weaning at Marion

Island from 1983 to 1990 (for more detail see Pistorius *et al.* 2000). We searched for tagged seals at all the beaches (32 along a 51.9-km coastline) at Marion Island once a week during the breeding season (mid-August to mid-November) and every 10 days during the moulting period (mid-November to mid-April) from 1983 to 1999.

8.2.2 Data analyses

To obtain survival estimates from females primiparous at the different ages we constructed encounter-history matrices separately from records of resighted seals that were seen to give birth for the first time when three, four, five and six years old. We combined five- and six-year-olds because of small sample sizes. The first sighting of a female breeding was treated as the first release effectively yielding a sample size of 147, 229, and 117 females for the three groups respectively. Multiple sightings in a year were regarded as a single sighting and seals were assumed to age by one year on 15 October which is the peak haul-out date for breeding females at Marion Island (Bester & Wilkinson 1994). Similar to previous demographic studies of the population, females seen from 15 September onwards (i.e., during the breeding season) were accepted to survive up to the parturition date. We used MARK (G. White, Colorado State University; White & Burnham 1999) to derive likelihood estimates of survival from the encounter-history matrices. The program provides parameter estimates for the Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965), and also for several models that are special cases of that model (Lebreton *et al.* 1992). We could not distinguish between mortality and permanent emigration. We consequently refer to survival as apparent rather than absolute, although emigration from the study site is expected to have a minor influence on the estimates (Hindell & Little 1988; see Pistorius *et al.* 1999a).

The two fundamental parameters in these models are: Φ = the survival probability for all animals between the ith and $(i + 1)$th sample $(i = 1, \ldots, k - 1)$, and p = the capture probability for all animals in the ith sample $(i = 1, \ldots, k)$.

To investigate potential costs of early breeding in terms of reduced future breeding rates, we constructed capture history matrices similar to the above but only using resight (recapture) data collected during the breeding seasons. First time matings in elephant seals occur at sea (Laws 1994) and virtually all females that haul out during the breeding season give birth (Huber 1987; Wilkinson 1992). Owing to the intensive and constant resight effort and high resighting rates during the study period we were therefore able to calculate resighting probabilities during the breeding seasons using MARK and interpret these as indices of breeding probabilities (see Pistorius *et al.* 2001).

The first step in the mark-recapture analyses involved Goodness of Fit (GOF) tests of the CJS model (full time-dependent model) using the program RELEASE (Burnham *et al.* 1987) to check whether the assumptions pertaining to the model were met (see Lebreton *et al.* 1992).

Proper model selection, which is the primary issue in the analysis of capture-mark-recapture (CMR) data (Anderson *et al.* 1994), was accomplished using the Akaike Information Criterion (AIC). AIC is a standard procedure for model selection in a CMR context, and it weighs the quality of fit (deviance) and the precision (via the number of parameters), so as to select the most parsimonious model that adequately describes the data (Lebreton *et al.* 1993; Anderson *et al.* 1994; Loison *et al.* 1994). It was used to select between the full time-dependent model and the constant capture- and/or survival-probability model (assuming no year-to-year changes in these parameters) for females breeding at the various ages. The model with the lowest AIC value was selected for each group.

Likelihood-ratio-tests (LRT) were used to test for age-effects on survival after first breeding at the respective ages. It was in addition used to test for significant differences in future survival and capture probability estimates between females primiparous at the different ages.

Although the elephant seal population at Marion Island has been confirmed to have relatively high tag retention rates (see Pistorius *et al.* 2000), they were nonetheless used to adjust all the survival estimates in order to account for the potential bias in estimates caused by tag loss.

8.3 Results

The CJS model fitted the data from females breeding for the first time at age three satisfactorily according to Test 3, females breeding for the first time at age four according to Test 3SR and females breeding for the first time at ages five and six according to Tests 2 and 3 (Table 17). It fitted the breeding season recapture data for all three groups according to Test 2 and Test 3 (Table 17).

We selected the constant survival and capture probability model as the most parsimonious one for females that gave birth first when three and four years old (Table 18). The full time-dependent model was the most suitable for females breeding for the first time when older than four (Table 18). Using only the breeding season recapture data, the most parsimonious model for first time breeders at age three and ages five and six showed constant survival and capture probabilities whereas first time breeders at age four showed time dependence in capture but not survival probability (Table 18).

We found no significant age effect on female survival after the first breeding event in females primiparous at age three ($\chi^2 = 1.58$, df = 4, p = 0.812) and age four ($\chi^2 = 1.23$, df = 3, p = 0.746) although such an effect was evident in females breeding at an older age ($\chi^2 = 5.52$, df = 2, p = 0.063). For females primiparous at ages three and four there was also no significant differences in survival in the year after giving birth for the first time when compared to later survival ($\chi^2 = 0.01$, df = 1, p = 0.933; $\chi^2 = 0.08$, df = 1, p = 0.776) although such a reduction in survival was evident for older primiparous females ($\chi^2 = 4.68$, df = 1, p = 0.031). Future survival did not differ significantly between females who gave birth when three versus four years old ($\chi^2 = 0.65$, df = 4, p = 0.957), neither between females giving birth when three versus five and six years old ($\chi^2 = 5.78$, df = 3, p = 0.123). The level of significance in the latter is low and this may be a reflection of the early primiparous females having greater probabilities of survival than females that first gave birth when older as is evident from Table 19.

There was no significant change in breeding probability after first breeding at age three ($\chi^2 = 3.50$, df = 4, p = 0.479), four ($\chi^2 = 6.86$, df = 4, p = 0.143) and older ($\chi^2 = 3.14$, df = 3, p = 0.371). No significant reduction in breeding probability the year following the first breeding event (relative to later probabilities of breeding) was evident for females primiparous at the respective ages (age three: $\chi^2 = 2.17$, df = 1, p = 0.141; age four: $\chi^2 = 1.92$, df = 2, p = 0.383; ages five and six: $\chi^2 = 1.01$, df = 1, p = 0.315). Although not significant, three-year-old and five- and six-year-old primiparous females had an approximately 5% lower breeding probability the year following primiparity relative to subsequent years.

We found no significant difference between future breeding probabilities of females primiparous at ages three and four (χ^2 = 5.83, df = 4, p = 0.212), nor between females primiparous at ages three and ages five and six (χ^2 = 0.87, df = 4, p = 0.928) (Table 20).

Table 17. Goodness-of-fit tests of the Cormack-Jolly-Seber model for southern elephant seal females breeding for the first time at different ages at Marion Island.

Age at breeding	χ^2	*df*	*P*
		Modelling survival probability	
3	5.30	3	0.151
4	6.34	3	0.100
5-	2.58	2	0.765
		Modelling capture probability (breeding season)	
3	10.98	8	0.203
4	9.57	7	0.215
5-	4.43	5	0.489

Table 18. Elimination of nonsignificant effects from the full CJS model in modelling survival and capture probability in southern elephant seals breeding for the first time at various ages at Marion Island: for each model the number of estimable parameters (np), the deviance (DEV), and the Akaike information criterion (AIC) are given. The value in bold denotes the most parsimonious model.

Age at breeding	*Model*	*np*	*DEV*	*AIC*
	Modelling survival probability			
3	(1) (ϕ_t, p_t)	11	42.08	703.69
	(2) (ϕ_t, p_c)	7	50.15	703.41
	(3) (ϕ_c, p_c)	2	52.50	**695.53**
4	(1) (ϕ_t, p_t)	9	100.64	1025.55
	(2) (ϕ_t, p_c)	6	103.48	1022.23
	(3) (ϕ_c, p_c)	2	106.74	**1017.38**
5 & 6	(1) (ϕ_t, p_t)	7	15.92	**476.17**
	(2) (ϕ_t, p_c)	5	26.16	480.05
	(3) (ϕ_c, p_t)	5	22.00	482.89
	Modelling capture probability (breeding season)			
3	(1) (ϕ_t, p_t)	11	44.09	828.35
	(2) (ϕ_c, p_t)	7	45.23	821.09
	(3) (ϕ_c, p_c)	2	50.86	**816.48**
4	(1) (ϕ_t, p_t)	9	26.65	1106.60
	(2) (ϕ_c, p_t)	6	30.93	**1104.72**
	(3) (ϕ_c, p_c)	2	39.87	1105.54
5 & 6	(1) (ϕ_t, p_t)	7	8.98	414.13
	(2) (ϕ_c, p_t)	5	11.17	412.05
	(3) (ϕ_c, p_c)	2	13.03	**407.66**

ϕ_t : Time-dependent survival rate
ϕ_c: Constant survival rate
p_t: Time-dependent capture probability
p_c: Constant capture probability

Table 19. Survival of southern elephant seal females giving birth for the first time at various ages at Marion Island (estimates from the age dependent model is presented in addition to estimates from the constant survival model (selected using AIC) in order to examine survival costs directly following first breeding).

	AIC selected model			*Time dependent survival model*		
Age	ϕ	*S.E.*(ϕ)	*p*	ϕ	*S.E.*(ϕ)	*p*
				Age at first breeding		
				Age 3		
4	0.756	0.020	0.911	0.742	0.038	0.914
5	0.756	0.020	0.911	0.748	0.045	0.914
6	0.756	0.020	0.911	0.812	0.049	0.914
7	0.756	0.020	0.911	0.763	0.059	0.914
8	0.756	0.020	0.911	0.753	0.071	0.914
9	0.756	0.020	0.911	0.680	0.093	0.914
				Age 4		
5	0.760	0.017	0.889	0.736	0.031	0.888
6	0.760	0.017	0.889	0.753	0.037	0.888
7	0.760	0.017	0.889	0.824	0.041	0.888
8	0.760	0.017	0.889	0.712	0.051	0.888
9	0.760	0.017	0.889	0.843	0.065	0.888
				Ages 5 & 6		
6, 7	0.609	0.052	0.760	0.609	0.052	0.760
7, 8	0.736	0.062	0.974	0.736	0.062	0.974
8, 9	0.823	0.063	0.897	0.823	0.063	0.897
9, 10	0.775	0.078	0.905	0.775	0.078	0.905

Table 20. Capture probabilities as indices of breeding probabilities for southern elephant seal females giving birth for the first time at various ages at Marion Island (estimates from the age dependent model is presented in addition to estimates from the constant capture probability model in order to examine the potential of early breeders skipping subsequent breeding opportunities).

	AIC selected model			*Time dependent survival model*		
Age	*p*	*S.E.(p)*	ϕ	*p*	*S.E.(p)*	ϕ
			Age at first breeding			
			Age 3			
4	0.739	0.029	0.737	0.686	0.048	0.741
5	0.739	0.029	0.737	0.794	0.052	0.741
6	0.739	0.029	0.737	0.741	0.063	0.741
7	0.739	0.029	0.737	0.839	0.062	0.741
8	0.739	0.029	0.737	0.660	0.100	0.741
9	0.739	0.029	0.737	0.657	0.136	0.741
			Age 4			
5	0.789	0.037	0.739	0.789	0.037	0.739
6	0.778	0.042	0.739	0.778	0.042	0.739
7	0.913	0.033	0.739	0.913	0.033	0.739
8	0.748	0.063	0.739	0.748	0.063	0.739
9	0.828	0.095	0.739	0.828	0.095	0.739
			Ages 5 & 6			
6, 7	0.733	0.038	0.733	0.677	0.060	0.721
7, 8	0.733	0.038	0.733	0.709	0.071	0.721
8, 9	0.733	0.038	0.733	0.768	0.073	0.721
9, 10	0.733	0.038	0.733	0.881	0.077	0.721

8.4 Discussion

Most life history models assume that reproduction is costly, and that reproductive events compromise future reproductive success and longevity, especially among young animals (e.g., Gadgil & Bossert 1970; Stearns 1976; Bell 1980). Consequently, southern elephant seal females that gave birth when three years old would be expected to have poorer future reproductive success (future survival and/or breeding probability) versus females who were primiparous later. However, we found no such effects on survival or on breeding frequency in the southern elephant seal population. Indeed, females primiparous when older (five and six years old) on average had a slightly higher (non-significant) mortality, and this was particularly evident following the year they first reproduced. Females primiparous at age four on average had a 7-8% higher annual future breeding probability than those primiparous at age three, although this was not significant. Annual female survival was about 76% and less than half the females surviving to primiparity would therefore breed on more than two occasions. The benefits of the above-mentioned increase in breeding probability relative to early primiparity therefore seem insignificant. No notable fitness costs in terms of future survival or breeding frequency associated with early breeding are therefore apparent in the southern elephant seal population at Marion Island. The above-mentioned life history theory postulate that early breeders subsequently have poorer reproductive success therefore appears to be unwarranted at least for the Marion Island elephant seal population.

Life histories are thought to be the end result of a variety of functional responses to different state variables that have varying degrees of influence (Boyd 2000). With equal future reproductive potential (in terms of survival and breeding frequency) of females primiparous at the different ages, we would expect mass (and hence condition) at primiparity to be similar among females primiparous at the different ages. In particular three-year-old females (but not excluding older primiparous females) which have not reached adult size (86% of ultimate body length; Laws 1956b), and are still actively growing, but breed, must bear at the same time the energetic costs of growth and reproduction. If three-year-old primiparous females in a food limited population (which appears to be the case for the Marion Island elephant seal population; Pistorius *et al.* 1999a) had lower body mass compared to older primiparous females, then they would have been expected to have significant relative reductions in future survival and/or reproduction (e.g., Festa-Bianchet *et al.* 1998; Pomeroy *et al.* 1999). Mass therefore appears to be the most important state variable influencing reproduction in southern elephant seals (Laws 1956b). Breeding in southern elephant seals is therefore likely to be determined by a critical threshold body mass (as is the case for some (Albon *et al.* 1983; Saether & Haagenrud 1983), but not all (Jorgenson *et al.* 1993), ungulate species) and once this is reached no further delay in the onset of reproduction, nor a trade-off between growth and reproduction, takes place. This study, therefore, lends support to the notion that in capital breeders, mass has a fundamental influence on reproductive potential (Festa-Bianchet *et al.* 1998; Pomeroy *et al.* 1999; Boyd 2000).

Pistorius *et al.* (1999a) documented a decline in survival of almost ten percent in three-year-old southern elephant seal females at Marion Island concurrent with a temporal shift in reproductive rates of the population (Pistorius *et al.* 2001). The proportion of three-year-old females being recruited into the adult population increased significantly over this period as a density dependent response in the declining population, concurrent with a presumed relative improved per capita prey availability to the survivors (Pistorius *et al.* 2001). The decline in survival of three-year-olds is consequently likely to have been a function of increased fecundity in this age-class (Pistorius *et al.* 2001), rather than a response to an overall decline in food availability (Pistorius *et al.* 1999a), and suggests a reproductive cost associated with early breeding. Over the period of the present study, a mean of roughly 30% of three-year-old females was recruited into the adult population (Pistorius *et al.* 2001). This group of females had a lower (76%) survival rate in their fourth year (present study), compared to 82% survival of all three-year-old females in their fourth year (Pistorius *et al.* 1999a), supporting the above notion. We nevertheless expect that females breeding at age three were in better body condition than those that did not breed at this age, as we cannot assess the cost of reproduction by comparing individuals that reproduce with those that do not as a result of likely individual differences in body condition (see McNamara & Houston 1996). However, females breeding at age three were able to bear the energetic cost of reproduction without a decrease in subsequent survival and reproductive frequency relative to older primiparous females (present study).

Similar studies on Antarctic fur seals and northern elephant seals demonstrated distinct future reductions in survival and fecundity as costs incurred through reproduction (Reiter *et al.* 1991; Boyd *et al.* 1995). Antarctic fur seals are income breeders, implying that breeding females rely mainly on energy obtained through foraging during the lactation period to wean their pups, whereas elephant seals are extreme examples of capital breeders, and females therefore rely entirely upon stored energy reserves to wean their pups (Jonsson 1997; Boyd 2000). Seals in these two breeding categories are likely to have contrasting life history determinants (Boyd 2000). Mass has been shown to be the dominant state variable influencing pregnancy in some phocids that are capital breeders, with it being less important in an income breeder, the Antarctic fur seal (Boyd 2000). The difference in fitness costs associated with breeding between the southern elephant seal and Antarctic fur seals could therefore be a reflection of the varying influence of mass on reproduction in capital and income breeding mammals. Conversely, an obscure dichotomy exists between the results from the present study for southern elephant seals and that found for northern elephant seals (both capital breeders).

The southern elephant seal population at Marion Island declined at an average annual rate of 5.8% over most of the study period (1986-1994) (Pistorius *et al.* 1999b; Chapter 5), and this decline was ascribed to prey limitation (Pistorius *et al.* 1999a). The northern elephant seal population, on the other hand, was increasing during studies of life history variables (Cooper & Stewart 1983; Le Boeuf & Reiter 1988; Reiter & Le Boeuf 1991). Despite this difference we counter-intuitively found no fitness costs in the southern elephant seal population where it is most likely to be manifested (as a result of food limitation), whereas researchers found several fitness costs associated with early breeding in northern elephant seals. One of these presumed fitness costs, reduced chances of pup survival, in northern elephant seals can be explained by resource limitation in the form of restricted space availability at the breeding beaches (Reiter *et al.* 1981). Fitness costs in terms of reduced future reproductive success and survival of early breeders has, however, also been documented (Huber 1987; Reiter & Le Boeuf 1991) and this begs explanation in view of the findings in the present study. Unlike the present study, it was also found that annual mortality rate was highest immediately following first reproduction irrespective of age (Huber 1987; Reiter & Le Boeuf 1991). Although reference is widely made to this work, the methods used to obtain the above results have been questioned on statistical and biological grounds and larger sample sizes have been recommended to reach sound conclusions (Sydeman & Nur 1994).

From the present study we would expect a positive correlation between growth, particularly in the first few years of life, and lifetime reproductive success and hence fitness in southern elephant seals. This concept has been supported for several species by the fact that faster-growing females begin reproducing earlier in life (Ozoga & Verme 1982; Saether & Haagenrud 1983). Natural selection is therefore likely to act primarily on early foraging behaviour and on factors influencing weaning mass in order to maximise individual fitness in southern elephant seals.

When evaluating the data in terms of meeting the underlying assumptions of the CJS model, the year-round data for three- and four-year-old primiparous females failed to pass the Test 2 component of the GOF test. This suggests heterogeneity in survival and/or capture probability within groups of individuals last released on the same sampling occasion. This heterogeneity (in resighting or survival probabilities) is often encountered in real data sets and it results in relatively small if any biases on survival rates since the analysis methods used have some robustness to heterogeneity (Carothers 1979; Nichols *et al.* 1982; Pollock & Raveling 1982; Burnham *et al.* 1987). It may, however, result in actual variances of estimates exceeding estimated theoretical variances (Burnham *et al.* 1987). The data from the breeding seasons only showed a reasonable fit to the CJS model. The survival estimates obtained from this data were very similar to those from the year-round data (2% difference for three- and four-year-old primiparous females and less than 1% difference for older primiparous females) and this is in support of the perception that heterogeneity results in small biases in estimates. Sample sizes in this study are notably larger than most previous studies of its kind (Festa-Bianchet 1989; Green & Rothstein 1991; Reiter & Le Boeuf 1991). The population, which has been declining over the past several decades, appeared food limited over the study period (Pistorius *et al.* 1999a). This is a condition required to invoke the full potential of possible fitness costs associated with early breeding since food abundance could mask any such costs (see Festa-Bianchet *et al.* 1998).

The reproductive success of a female can be measured as the number of successful offspring she manages to produce throughout her life span. It comprises several interdependent aspects, including survival and longevity of the female, the age of primiparity and subsequent breeding probabilities and the survival of the offspring. In this study we have discounted fitness costs incurred through reproductive expenditure in terms of a relative reduction in future breeding probabilities and survival, at least up to age nine. A senescence effect (in terms of declining reproduction and survival with age) does not appear prevalent in the population (Chapter 6) and we therefore expect age-specific post-primiparous reproductive participation to be equal among females primiparous at the respective ages.

An aspect of fitness we have not dealt with is the successful weaning of pups from variously aged females and their future survival. In several phocid species, including southern elephant seals, larger females tend to produce pups that are larger both at birth and at weaning (McCann *et al.* 1989; Bowen *et al.* 2001). Moreover, size, and therefore condition at weaning, have been shown to influence first year survival in southern elephant seals at Macquarie Island (McMahon *et al.* 2000) and in grey seals (Hall *et al.* 2001) although no such relationship was evident for northern elephant seals (Le Boeuf *et al.* 1994). Delaying the onset of reproduction by a year in order to invest in growth rather than reproduction (Reiter & Le Boeuf 1991) may therefore increase the probability of survival of the offspring. With the exceptionally low pre-weaning mortality in elephant seals at Marion Island (3.8%; Chapter 3), a fitness cost in terms of reduced offspring survival associated with early primiparity would presumably entail reductions in post-weaning and first year (McMahon *et al.* 2000) and juvenile survival (Coulson *et al.* 1997; Reed & Plante 1997). Unlike adult females, juveniles (ages 0-2) at Marion Island do not appear to be food limited since the survival of these animals have been constant over time irrespective of changes in population growth rate (Chapter 4), although adult females wean their pups at significantly lower mass here (Marion Island) than at other sites (e.g., Macquarie Island) in the southern ocean (Burton *et al.* 1997). We consequently do not suspect differences in weaning mass of pups from females primiparous at different ages to greatly influence survival in this population component. In the absence of future fitness costs incurred through early primiparity (this study), we argue that even if offspring survival of young primiparous females is lower than that for older primiparous females, the high overall future chances of offspring survival (although possibly slightly lower than in older primiparous females; McMahon *et al.* 2000; Chapter 4) and the experience gained from the first reproductive event, would presumably curtail any potential fitness cost associated with early breeding. The influence of weaning mass on future survival of elephant seals at Marion Island does, nonetheless, require investigation.

In conclusion, we concur that mass, and hence condition, is the most important variable influencing the age of primiparity in a capital breeder such as southern elephant seals (Laws 1956b; Boyd 2000), and that no delay in reproduction takes place once the critical breeding mass has been achieved. We found no evidence that future fitness costs are incurred through reproductive expenditure in southern elephant seals.

CHAPTER 9 FITNESS CONNOTATIONS OF THE WINTER HAUL-OUT BY SOUTHERN ELEPHANT SEALS AT MARION ISLAND

9.1 Intoduction

Between the annual moult, which is obligatory for all age classes, and the following breeding season, immature elephant seals (*Mirounga* spp.) of either sex (and infrequently adults too) haul out on land on one or more occasions for periods of a few days up to several weeks at a time (Laws 1956, Carrick *et al.* 1962, Odell 1974, Condy 1979, Stewart & Yochem 1984, Hindell & Burton 1988). This terrestrial phase takes place during the austral autumn and winter in southern elephant seals, *M. leonina* (Laws 1956, Carrick *et al.* 1962, Le Boeuf & Laws 1994), and the boreal autumn (fall) in northern elephant seals, *M. angustirostris* (Odell 1974, Stewart & Yochem 1984, Le Boeuf & Laws 1994). Hereafter referred to as the winter haulout for convenience sake (after Hofmeyr 2001), animals participating in this haulout are said to "winter".

It is not clear what the purpose of the winter haulout is, or whether it is obligatory for all immature individuals. It appears less prevalent in some southern elephant seal (*M. leonina*)

(Laws 1994).

In this study, future survival and capture probabilities of juvenile male and female southern elephant seals that wintered at Marion Island (46°54'S, 37°45'E), are estimated. Their survival and capture probabilities are compared to those of individuals not seen to winter, over the same periods. This was done to assess whether there are any fitness connotations to the winter haulout.

9.2 Methods

A total of 1342 (average: 224, range: 200-243) male and 1341 (average: 224, range: 200-249) female elephant seal pups were double tagged in their hind flippers after weaning from 1990 through 1995 on Marion Island, using uniquely numbered, colour-coded Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom) (for more detail see Pistorius *et al.* 2000). For the period 1990-2000 all the beaches (32 along a 51.9-km coastline) were searched for tagged seals every 10 days during the moulting period (mid-November to mid-April) and during the winter haul-out (June, July and August). For each tagged seal that was resighted, attempts were made to record the tag number and colour combination, the number of tags remaining (one or two) and date of sighting. The resight data were entered and stored electronically in a database.

The moult haulout is obligatory for all age classes older than underyearlings, and is not subject to individual or age related variation in haulout probability as the winter and breeding phases apparently are. Thus capture history input files were created only from recapture data collected during the moulting season. The input constituted recaptures during the moulting season of animals that wintered at Marion Island in their first, second and third year of life, and marked individuals of corresponding ages not observed to winter. Multiple sightings in a year were treated as a single sighting and seals were assumed to age on the 15th of October (see Pistorius *et al.* 1999a). Using the software program MARK, survival and capture probabilities for the second and third year of life were obtained (separately for males and females) for the two groups of seals. These two fundamental parameters are denoted as follows: Φ = the survival probability for all animals between the ith and $(i + 1)$th encounter occasion ($i = 1, \ldots, k-1$), and p = the capture probability for all animals in the ith encounter occasion ($i = 1, \ldots, k$).

Survival and capture probabilities subsequent to the year when individuals' presence or absence during the winter phase was noted, were estimated. Using the program RELEASE, goodness of fit tests (see Lebreton *et al.* 1992, Pistorius *et al.* 1999a) were performed to see whether the data met the underlying assumptions of the Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965).

I tested for age-dependence in capture probability using the Akaike Information Criterion (AIC). AIC is a standard procedure for model selection in a CMR context, and it weighs the quality of fit or deviance (defined as the difference in –2Log (Likelihood) of the current model and –2Log(Likelihood) of the saturated model) and the precision (via the number of parameters), so as to select the most parsimonious model that adequately describes the data (Anderson *et al.* 1994). Juvenile survival over the first three years of life is age-dependent (Chapter 4) and we consequently did not attempt to reduce the number of survival parameters to be estimated.

I used Likelihood Ratio Tests (LRT) to test for significant differences between estimates from the wintering and non-wintering elephant seals.

9.3 Results & Discussion

Approximately 54% of the male (*n* = 376 of 699) and female (*n* = 411 of 762) marked seals known to have survived their first year, were observed to winter in that year. About 85% of males (*n* = 283 of 334) and 80% of females (*n* = 320 of 395) known to have survived their second year were observed to winter in that year and about 82% of males (*n* = 171 of 209) and 42% of females (*n* = 114 of 271) known to have survived their third year were observed to winter in that year. While a 100% recapture rate of animals that hauled out in autumn-winter or during the moulting period is unlikely, this rate should have been closely approximated due to the rigorous recapture program (Bester 1988, Pistorius *et al.* 1999a) and the ease with which tags of juveniles are read as a consequence of their small sizes.

The CJS model fitted the data for the majority of groups (Table 21). It did not, however, fit the data from males not wintering at age 0, males wintering at age 2 and females not wintering at age 0. We expect this to be a result of heterogeneity in recapture probability (see Lebreton *et al.* 1992).

In most cases capture probability was not age-dependent (Table 22).

Table 21. Goodness-of-fit tests of the Cormack-Jolly-Seber model by wintering and non-wintering southern elephant seal males and females at Marion Island (W = Winter; NW = Not wintering).

At age		*Males*			*Females*	
	χ^2	*df*	P	χ^2	*df*	*P*
0 (W)	3.97	1	0.100	0.91	2	0.636
(NW)	11.49	1	<0.010	2.75	2	<0.010
1 (W)	4.75	2	0.102	5.73	2	0.120
(NW)	4.60	2	0.100	1.51	2	0.469
2 (W)	7.95	2	0.019	1.01	2	0.604
(NW)	2.15	2	0.342	5.55	2	0.107

Table 22. Elimination of nonsignificant effects from the full CJS model in modelling survival of elephant seals seen to winter and those not seen to do so at Marion Island in their first three years of life: for each model the number of estimable parameters (np), the deviance (DEV), and the Akaike information criterion (AIC) are given.

Age	*Model*	*np*	*DEV*	*AIC*
		Males		
		Wintering		
0	(1) (ϕ_t, p_t)	5	14.89	1234.95
	(2) (ϕ_t, p_c)	4	16.58	**1234.61**
1	(1) (ϕ_t, p_t)	5	5.15	943.64
	(2) (ϕ_t, p_c)	4	6.35	**942.82**
2	(1) (ϕ_t, p_t)	5	8.66	586.75
	(2) (ϕ_t, p_c)	4	9.99	**586.03**
		Not wintering		
0	(1) (ϕ_t, p_t)	5	24.01	**1057.70**
	(2) (ϕ_t, p_c)	4	26.75	1058.40
1	(1) (ϕ_t, p_t)	5	6.93	180.81
	(2) (ϕ_t, p_c)	4	6.93	**178.60**
2	(1) (ϕ_t, p_t)	5	4.31	137.26
	(2) (ϕ_t, p_c)	4	4.67	**135.36**
		Females		
		Wintering		
0	(1) (ϕ_t, p_t)	5	1.56	**1310.71**
	(2) (ϕ_t, p_c)	4	3.69	1310.82
1	(1) (ϕ_t, p_t)	5	6.28	1005.76
	(2) (ϕ_t, p_c)	4	7.72	**1005.17**
2	(1) (ϕ_t, p_t)	5	1.05	371.27
	(2) (ϕ_t, p_c)	4	2.34	**370.49**
		Not wintering		
0	(1) (ϕ_t, p_t)	5	31.25	1163.26
	(2) (ϕ_t, p_c)	4	33.23	**1163.22**
1	(1) (ϕ_t, p_t)	5	2.06	251.75
	(2) (ϕ_t, p_c)	4	2.33	**249.89**
2	(1) (ϕ_t, p_t)	5	5.84	513.23
	(2) (ϕ_t, p_c)	4	5.88	**511.22**

ϕ_t : Time/age-dependent survival rate
p_t: Time/age-dependent capture probability
p_c: Constant capture probability

Marion Island that wintered during their first year of life compared to those not observed to do so (only moulting recaptures).

	Wintering				*Non-wintering*			
Age	ϕ	*S.E.(ϕ)*	*p*	*S.E.(p)*	ϕ	*S.E.(ϕ)*	*p*	*S.E.(p)*
Males								
Age 0								
1	0.793	0.024	0.854	0.019	0.862	0.042	0.601	0.041
2	0.773	0.030	0.854	0.019	0.700	0.053	0.708	0.048
Age 1								
2	0.791	0.026	0.904	0.018	0.790	0.074	0.821	0.061
3	0.740	0.032	0.904	0.018	0.573	0.088	0.821	0.061
Age 2								
3	0.774	0.036	0.875	0.028	0.881	0.066	0.882	0.055
4	0.719	0.045	0.875	0.028	0.659	0.092	0.882	0.055
Females								
Age 0								
1	0.832	0.021	0.876	0.021	0.841	0.027	0.785	0.024
2	0.757	0.027	0.920	0.021	0.727	0.035	0.785	0.024
Age 1								
2	0.796	0.024	0.937	0.013	0.726	0.055	0.908	0.036
3	0.786	0.028	0.937	0.013	0.741	0.066	0.908	0.036
Age 2								
3	0.798	0.040	0.916	0.025	0.800	0.034	0.782	0.022
4	0.765	0.048	0.916	0.025	0.768	0.041	0.782	0.022

Although there were differences between age-specific survival rates of wintering and non-wintering seals, none of these were significant (Table 23). Males and females wintering in their first year and females wintering in their third year had significantly higher future capture probabilities relative to non-wintering seals (Table 23). All wintering first-years had in excess of 9% higher future capture probability. From our data, there is no evidence that differences in winter haul-out participation are reflected in survival, and therefore we remain unsure whether there are any improved fitness associated with wintering behaviour. The differences in subsequent capture probabilities during moulting between wintering and non-wintering individuals (in their first, and females in their third year) at Marion Island strongly point to differential levels of philopatry between the two groups with lower levels evident in the latter. Hence age- and sex- related differences in participation levels, as deduced from observations of marked animals (Kirkman *et al.* 2001) may also have contributed to differences in philopatry within age- and sex-classes. Juveniles readily move between the proximate Marion and Prince Edward islands, with some ranging as far afield as Îles Crozet approximately 1000 km distant where they haul out for the autumn "resting" phase (Bester 1989). Juveniles not seen to haul out at Marion Island during the winter are therefore likely to have hauled out at other sites such as proximate Prince Edward Island.

Life history parameters for the southern elephant seal population at Marion Island have predominantly become available by applying variations of the CJS model to mark-recapture data (i.e. Pistorius *et al.* 1999; 2001). Recapture data for CJS analyses should meet several of the model's underlying assumptions. One of these states that all individuals in a cohort that were last released at the same occasion must be equally prone to recapture. Recapture data from the Marion Island population has shown some departures from the CJS model (see Pistorius *et al.* 1999a). The present study provides evidence that not all individuals of a cohort have equal capture probability. This amounts to a failure of the data to meet the equal captures probability assumption. Separating out recapture data from juveniles seen to haul out during the winter period from those not seen and analyzing the data separately is likely to reduce violation of the above-mentioned model assumption.

CHAPTER 10 CONCLUSIONS

Pre-weaning pup mortality in southern elephant seals at Marion Island has been consistently low, averaging less than 4% during the past 14 years at least, and it has been constant regardless of number of births and number of females at peak season (as an index of density). There was no evidence of a compensatory increase in pup survival as the population declined, also arguing against density-dependent influences on pre-weaning pup survival. The exceptions to particularly high pup survival were at beaches attended by small numbers of young, inexperienced and primiparous females, which may also have been occupied by younger adult males that may cause greater disturbance to mothers and pups than at other sites. Consequently, changes in pre-weaning pup survival can not account for the decline in the Marion Island elephant seal colony in recent years, owing to the relatively constant and consistently high survival of pups to weaning.

Juvenile survival over the first three years of life did not show significant changes with the stabilisation of the declining population of elephant seals. Survival of this population component therefore appears to have been inconsequential in the population decline at Marion Island. In addition, no gender or time effect was evident in juvenile survival.

Adult female survival explicitly responded to population growth rate and we therefore conclude that adult female survival, rather than juvenile survival, is the major regulating agent in the Marion Island population. An eight-percent increase in prime-age adult female survival was associated with a halt of a 5.8 % annual rate of decline at Marion Island, whereas a 6% higher adult female survival in the Peninsula Valdés population (compared to the stable Marion Island population) was associated with a 3.6% annual rate of increase. Similar causative factors have been proposed (Hindell *et al.* 1994) for the declines of southern Indian and Pacific Ocean southern elephant seal populations (including Îles Kerguelen and Macquarie Island), and the above conclusion about adult female survival may therefore be relevant to these populations.

There was no evidence for a senescence effect in terms of either reduced survival or diminishing breeding probabilities with age in southern elephant seal females. Mortality over the various age classes therefore resulted in no individuals surviving to the age where physiological decline would become a mortality agent or result in failure to breed. Very few previous longitudinal studies have reported on senescence due to the inherent difficulties associated with obtaining sufficient data to permit reliable estimation of demographic parameters of old individuals.

A significant increase in pubescent male survival of between 4.4 and 6.3 percent was associated with the halt in the decline of the southern elephant seal population at Marion Island. These animals have particularly high energetic requirements as a result of a secondary growth spurt. This increase in survival concurrent with the population stabilisation therefore lends support to the food limitation hypothesis. In addition, I found a distinct three-year pattern in pubescent male survival with survival in each third year showing a substantial relative reduction. This appears to be correlated with ENSO events but I have not identified causal links between environmental changes and changes in growth rate in the southern elephant seal population.

Reproductive expenditure did not reduce future reproductive potential in the elephant seal population at Marion Island. The future annual survival of females breeding at age three (76%), which is the youngest age of primiparity in southern elephant seals, was the same as that for females primiparous at age four and slightly, although not significantly, higher than that for females primiparous at ages five and six (74%). There was, in addition, no reduced survival in the year following first breeding in young first time breeders although there was for older first time breeders. Annual future breeding probabilities of females primiparous at age three was not significantly different to those from females primiparous at an older age. I found no evidence for the life history theory prediction that any reproductive expenditure entails future fitness costs. I consequently conclude that age of primiparity in southern elephant seal females is determined by the acquisition of a critical body mass, after which no further delay in reproduction takes place.

Southern elephant seals haul out on land to moult and to breed and the socio-ecological aspects of this behaviour has been well documented. A third haulout, which is referred to as the winter haulout, has received minimal attention and reasons for this haulout remain obscure. I found no significant differences in survival between wintering and non-wintering elephant seals suggesting that survival is not a fitness correlate of this behaviour. I did, however, find that seals of both sexes wintering in their first and females in their third year at Marion Island had significantly higher future capture probabilities relative to non-wintering seals. I thereby provide unique evidence of differential site fidelity within age- and sex classes, which has implications for population modelling.

Several aspects of the population biology of southern elephant seals at Marion Island still require investigation. It is of importance to monitor the fate of juvenile elephant seals weaned at different weights so as to establish whether weight at weaning influences future survival and reproduction. If a positive relationship between weaning weight and future fitness is established it will be important to determine whether older, and perhaps heavier females give birth to larger pups. This will be necessary to confirm conclusions reached about life history aspects of breeding in this study. The tagging and monitoring of female pups from females primiparous at known ages will also allow the assessment of the genetic extent of age of primiparity.

Long-term ecological data is of extreme importance for the purpose of elucidating patterns and processes in nature, as well as for understanding cause and effect relationships. Long-term monitoring of populations is indeed the only means whereby we can achieve a comprehensive understanding of the dynamics governing these populations. The continued mark-recapture program on elephant seals at Marion Island is thereby of paramount importance to further our understanding of the dynamics of this intensively studied marine mammal population. Following a typical predator-prey relationship, I expect to see an increase in the growth of the population in the near future, as the population presently appears to have temporarily stabilised at the lowest level recorded in the past five decades. This will provide a great opportunity to monitor the changes in vital rates associated with the anticipated increase in population growth rate and may lend further credence to conclusions reached in this study.

Similar causative factors have been proposed (Hindell *et al.* 1994) for the declines of southern Indian and Pacific Ocean southern elephant seal populations (including Îles Kerguelen and Macquarie Island), and results that emanated from this study are likely to bear strong relevance to these other populations. It is nonetheless important to caution against generalisations that are too stringent since the different populations do succumb to different circumstances. This is evidenced by the fact that the Marion Island elephant seal population continued to decline in numbers for several years after the decline in the Kerguelen population was halted (Guinet *et al.* 1999), despite the two populations having been assigned to the same stock of southern elephant seals (see Laws 1994).

This study has aided the understanding of the demographics of a southern elephant seal population, with likely relevance to other populations. The proximate cause for the long-term population decline, low adult female survival, was identified. We speculate that food availability was ultimately related to the decline. Research on the dynamics of the Southern Ocean, particularly the predator-prey relationships relating to southern elephant seals, and large-scale environmental processes causing shifts in these relationships, is required to further advance our understanding of this apex predator.

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APPENDIX 1

THE DISTRIBUTION, MOVEMENT, AND POPULATION SIZE OF KILLER WHALES (*ORCINUS ORCA*) AROUND MARION ISLAND, SOUTHERN OCEAN

Killer whales (*Orcinus orca*) have a highly cosmopolitan distribution and are found in most of the world's oceans. They do, however, show a preference for the cold coastal waters of the Arctic and Antarctic Oceans and are widespread in the Indian Ocean (Dalheim 1981; Heimlich-Boran 1988; Leatherwood *et al.* 1984). Killer whales are most abundant around Marion Island during October through December (Condy *et al.* 1978; Keith *et al.* 2001), which has been related to the southern elephant seal (*Mirounga leonina*) breeding season and the haul out pattern of certain penguin species (Condy *et al.* 1978). A similar trend was found at the Îles Crozet (Guinet 1991; Ridoux 1986) which is situated in the same latitudes.

A recent study reported on the status of the killer whale population at Marion Island over a 22 year period (1973-1996), focusing on the temporal and spatial occurrence of killer whales in near shore waters and photo-identification of individuals (Keith *et al.* 2001). A limitation in this study was the opportunistic nature of most of the observations and the fact that dedicated shore-based observations were made from the Marion Island base-station only. In the present study simultaneous killer whale observations were performed at several points around the island to obtain an improved view of the temporal and spatial occurrence of killer whales around the island. In addition, I attempt an estimate of the population size of killer whales during their peak period of occurrence around Marion Island, describe their local movements, and report on previously unidentified individuals.

Marion Island (46°54'S, 37°45'E) is situated in the Southern Indian Ocean north of the Antarctic Polar Front. The island has an area of 296 km^2 (Condy *et al.* 1978) with a circumference of approximately 90 km (Wilkinson 1992). Shore-based observations were made using binoculars from eight locations around the island which covered areas where killer whale activity had been most frequently observed in the past (Keith *et al.* 2001) but also to give a relatively even spread around the island (Fig. 7). The south-westerly section of the island was excluded as very few killer whale sightings had been recorded here (Keith *et al.* 2001). During a single day (13/12/2000) in the peak killer whale season at Marion Island (see Keith *et al.* 2001), dedicated observations were made from 06h00 to 18h00 Local Apparent Time (GMT + 2) from all eight locations simultaneously. On a second day (23/12/2000) dedicated observations were made from 06h00 to 12h00 at four locations on the east coast while at the base station observations were made from 06h00 to 18h00. For each observation the number of killer whales in the pod, sex and age class of individuals (where possible), time of arrival, direction of travel, distance from the shore and duration (watches of all observers were synchronised) of observation. Sex and age were subjectively determined by using body size and size and shape of the dorsal fin following Leatherwood *et al.* (1976). Individuals were assigned to one of four age classes: adult, sub-adult, calves and unidentified. Four different near shore zones were established following Condy *et al.* (1978): Zone 1: Within 5 meters of the shore; Zone 2: 5 to 100m from the shore, usually extending to the first belt of kelp (*Macrocystis* sp.); Zone 3: 100m to 500m from the shore, usually extending to the second belt of kelp; Zone 4: beyond 500m from the shore.

The spatial distribution and movement of killer whales (around the island as well as distance from the shore) were plotted on a map of Marion Island and a histogram of their temporal distribution during the 12-hour observation period, divided into 10-minute intervals, was constructed. Swimming speed was estimated from the movement of single pods between two adjacent observation points. I only used data points when pods were reliably matched based on pod composition, the zone they were swimming in as well as movement of other pods in the area over the same time period. Pods were excluded when departure and arrival times of members within the pods at two observation points were staggered by more than 5 minutes at each end. The distance between two observation points was determined from a scaled 1:50 000 topographical map of Marion Island. I used two distances; a coastal (maximum) distance, which incorporated all inlets and small bays, and a minimum distance, which ignored such indentations of the general coastline. As a result minimum and maximum swimming speeds are presented.

I used several methods to acquire estimates of population size. Firstly I attempted to identify all the unique pods sighted during the day and I totalled the individuals of the respective pods to give us a minimum estimate. Pods were identified by using the number of individuals in the pod, pod composition, direction and zone of travel and time of observation. Secondly I tracked movement of the respective pods during the day and by excluding overlap of individuals totalled the number of individuals. If a total of 10 were, for example seen moving south past the base station and in the same time interval 10 were seen moving north past Ship's Cove I obtained a lower population estimate of 20 individuals. In the third approach, I used the most individuals sighted in ten-minute intervals during the course of the day (taken from the temporal frequency distribution histogram - see below). Throughout the three months (October to December 2000) of peak killer whale activity, observations were done opportunistically and team members recorded, and where possible photographed, previously recorded individuals (based on unique fin markings – see Keith *et al.* 2001).

On the first day of observation 260 individuals were recorded around the island and not one on the second day of observation. The resultant distribution of killer whales in near shore waters around Marion Island is shown in Fig. 8. All killer whale sightings, except one, were made from the four observation points on the northeast coast (Fig. 7). The single observation (one individual) was made at Kildalkey Bay (southeast coast). The relatively large number of elephant seals (recently weaned pups from the breeding season and yearlings and sub-adults hauling out to moult - see Condy 1979; Kirkman 1999) on the east coast relative to the rest of the island (Condy 1977; Wilkinson and Bester 1990) probably explains the large number of sightings of killer whales recorded here. Although the most sightings were recorded where the resight effort (number of observation localities) was the greatest (northeast coast), the virtual absence of killer whales at Kildalkey Bay, the largest single colony of king penquins and elephant seals on the island, suggests that on the day at least, the northeast coast was favoured. Elephant seals also occur on the south and north coasts but are not nearly as numerous as on the east coast (Condy 1977; Hofmeyr 2001).

We observed 39.6% of individuals in Zone 1, 32.7% in Zone 2, 7.7% in Zone 3 and 20.0% in Zone 4. Movement in Zones 1 and 4 falls within the range recorded by Keith *et al.* (2001) as were the combined frequency of occurrence of killer whales in zones 2 & 3. As noted in Keith *et al.* (2001), Zone 1 is likely to be the most rewarding hunting area for killer whales since it is here where elephant seal pups remain during play and local post-weaning dispersion (Panagis 1981; Lenglart and Bester 1982; Wilkinson and Bester 1990). Most of the presumed kills (deduced from large numbers of giant petrels and kelp gulls surrounding killer whale activity) sighted during the year (*n* > 20) were, however, in Zones 3 and 4. Killer whales were occasionally seen moving with their prey and we suspect that the prey is often seized in near shore waters and is then moved further out to sea.

Using a nonparametric Kolmogorov-Smirnov test, I found no significant variation ($p > 0.10$) in the number of killer whales sighted per hour (expressed as a percentage) throughout the day (Fig. 3) as did Keith *et al.* (2001) based on a much larger (~12 days) sample. There was a high peak in the percentage frequency occurrence of killer whale sightings between 15:20 and 15:40, reminiscent of the (statistically non-significant) peaks found in early morning and late afternoon by Keith *et al.* (2001), which appeared to be a convergence of a large number of pods offshore from the base station. Such a convergence of pods was occasionally ($n > 10$) seen during the months of peak killer whale activity. It frequently revolved around freshly killed prey, as identified from the large number of scavenging birds that were attracted to these sites. On one occasion two pods with four and seven individuals respectively (approaching from different directions) converged on a single king penguin, which they co-operatively cornered against a cliff face and then devoured. In another two instances a large number of killer whales (n = 10-20) was associating (non-violently) with a few passing humpback whales (a rare sighting from Marion Island) for an extensive time period. On several occasions, an aggregation of pods, as described above, resulted in large numbers of killer whales being observed from the base station in Zone 4. They remained in a large group with minimal movement or activity and it appeared to be some "gathering" of numerous, and potentially all, the pods around Marion Island. Keith *et al.* (2001) recorded a maximum of 28 killer whales per group (as opposed to pod) and we contend that this could conceivably be a "gathering" similar to those described above. It is also conceivable that this count approximated the population size at the time.

The absence of killer whale sightings on the second day of observation in late December, despite the opportunist sighting of three pods the previous day, suggested that the end of their peak season (declining activity through January and February – Condy *et al.*

1978; Keith *et al.* 2001) has approached. There therefore seems to be a high level of synchronisation in movement away from the island at the end of their peak season. In support, Roux (1986) found a clear seasonal cycle of occurrence at the temperate, low latitude Amsterdam Island with killer whales being rare in July to August, and more common in February to March (i.e., three to five months later than their peak in abundance around Marion Island and the Îles Crozet). The observed difference in the timing of peak abundance of killer whales might therefore be related to dispersing killer whales passing through different latitudes at different times (Mikhalev *et al.* 1981; Keith *et al.* 2001). The above observations support the notion that a strong social bond exists between the pods frequenting Marion Island waters, although an incontestable counter-argument could claim that an environmental cue is responsible for this sudden departure.

I identified seven individual pods (numbered 1-7 in Fig. 8) during the early morning to late afternoon sightings, with a total of 26 individuals. Pod identification was to a large degree subjective, but by using a parsimonious approach and making use of the set of criteria mentioned in the methods section I attempted to reduce the chances of identifying specific pods as separate pods. Several sightings were recorded that could not be attributed to one of the above seven pods due to different assessments by observers at various observation points of pod size, composition, direction of movement or time sighted. The population estimate derived from this method is therefore likely to be a minimum estimate. Using the second method, between 15h28 and 17h55, 29 individuals moved north past the base station and this represents the second estimate. Although about 20 individuals were seen moving in a general northerly direction just prior to this I did not include them as they were seen in Zone 4 and are likely to have been included in the subsequent northward moving groups. In the third approach, the estimates of population size around Marion Island were derived from the two peaks in the frequency histogram (Fig. 9). At the 15h20-15h30 peak 20 individuals were seen in front of the base station, 3 individuals at Archway and at 16h02, three individuals were seen approaching from the west at Pinnacles (which would preclude overlap) yielding a total of 26 individuals. In the frequency histogram four individuals that were seen at the base at 15h30 are included in the total of 30 but these are likely to have been part of the 15h25 group of 20 and are hence not included in the estimate of 26. At the 16h50-17h00 peak 13 individuals were observed moving northwest past the base station and eight individuals west past Pinnacles at 16h52. Another three individuals moved west past Pinnacles at 17h08 yielding a total of 24 individuals. From the above, I estimate the population of killer whales around Marion Island during their peak season to be in the region of 25-30 individuals, assuming no major daily variation in numbers during the peak season.

Prey distribution and availability undoubtedly play a role in the high frequency of occurrence of killer whales at certain localities around the island (Keith *et al.* 2001). It is tempting to speculate that a higher elephant seal movement on the northeast coast could have a concentrating effect on killer whales in that particular area, to the exclusion of all other areas (present study). However, physical environmental conditions (such as sightability, the leeward position of the northeast coast, wind direction, etc) and social factors facilitating aggregation of killer whales, could have contributed. Despite the large number of fur seals (*Arctocephalus tropicalis*) residing on the west (e.g. Mixed Pickle Cove) and north coasts (e.g., Cape Davis) of Marion Island (Hofmeyr *et al.* 1997), no sightings of killer whales were recorded there on the day (present study). This might be related to the behaviour, distribution and difference in the seasonal haulout cycle of these two (of three) seal species found at Marion Island (Keith *et al.* 2001).

The adult elephant seal population has arguably been regulated through food availability (Pistorius *et al.* 1999b). Similarly, the high first year survival of elephant seals at Marion Island (Bester & Wilkinson 1994; Pistorius *et al.* 1999b) militates against killer whales making a profound impact, although Guinet *et al.* (1992) found a high predation rate of killer whales on weaned elephant seal pups at the Îles Crozet, with 25% of pups weaned on a particular beach being taken, and the actual predation probably being even higher. The persistently high, constant juvenile survival despite the decline (to 1994) and subsequent stabilization of the elephant seal breeding population at Marion Island (Pistorius *et al.* 1999a,b) bolsters the argument. An adult killer whale consumes in the region of 250kg of flesh daily (http://www.seaworld.com), and with 25-30 killer whales frequenting Marion Island waters during the elephant seal breeding season, they do have the potential to have a significant influence on the elephant seal population. It is likely that a large part of the 40% mortality in first years is attributable to killer whale predation but it appears that mortality resulting from predation has been constant over time and that it has not been influential in causing changes in population growth of the elephant seal population at Marion Island.

Using movement of 18 pods between two adjacent observation points I estimated swimming speeds to vary between 11.9 km h^{-1} and 14.44 km h^{-1}. A pod would therefore be able to patrol the entire island coastline in about 6.5 hours and the east coast in about 3 hours. This mobility of the killer whale pods frequenting inshore waters around Marion Island also suggests that the summer population of killer whales could on occasion be found concentrated in the same area, whether by design or by chance.

No known individuals with unique fin markings (Keith *et al.* 2001) were observed in the present study. As these individuals were originally described from photographic material taken as early as 1975 through 1989, it is likely that significant changes in population composition have taken place, although one individual was recognised over a period of 22 years (Keith *et al.* 2001). Definitely two and possibly four undescribed individuals with unique fin markings were identified and pictures of dorsal fins of these individuals have been posted on the Marion Island website (http://www.geocites.com/kildalkey). Team members participating in the annual expeditions to Marion Island will be tasked to continue collecting digital images of killer whales with fin markings to facilitate individual recognition and to update the website accordingly.

I urge future team members to participate in the collection of data similar to that which this study has been based on. A large enough sample size of simultaneous round-island observations will allow for the assessment of variability in movement patterns, which is required in order to make observations and monitoring from a single point meaningful.

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Figure 7. Observation points and percentage occurrence of killer whale sightings recorded during morning to afternoon observation at Marion Island.

Figure 8. Movement patterns of killer whale pods around Marion Island.

Figure 9. Frequency histogram of killer whale sightings around Marion Island.

APPENDIX 2

USING A STOCHASTIC MODEL TO EVALUATE THE IMPACT OF VITAL RATES ON POPULATION GROWTH IN SOUTHERN ELEPHANT SEALS AT MARION ISLAND

Here I assess the influence that the respective vital rates have on population growth using a stochastic model. My first aim is to compare the distribution of growth rates as predicted from the population model to the actual rates that were determined from annual counts of females and pups during the peak breeding seasons over the study period (see Wilkinson 1992 & Pistorius *et al.* 1999b). Secondly, I aim to measure the contribution of the different vital rates to changes in population growth. In particular, I attempt to tease apart the respective contributions of adult female survival and fecundity to population growth rate. These parameters have been reported to be instrumental in influencing recent changes in population growth of the southern elephant seal population at Marion Island (Pistorius *et al.* 1999a; Chapter 5), and their respective influences on population growth have in general been a subject of controversy (Gaillard *et al.* 1998).

I only modelled the female population as southern elephant seals are extremely polygamous and males are not expected to influence the growth of this population (Bester & Wilkinson 1994). The proportion of females in the population was calculated from the average of the proportions recorded annually from the 1989 to 1992 standing age-distributions (see Pistorius *et al.* 1999b). The proportion of females in each age class was similarly obtained from these age-distributions.

Seven age classes were modelled: ages zero to five separately, and age six and up as a single age-class. From age six all females are recruited into the adult population and are expected to have similar survival (Caughley 1977; Pistorius *et al.* 2001), with no apparent senescence effect on survival or fecundity (Chapter 8).

No density-dependence in survival or fecundity was assumed. This was accounted for indirectly as I modelled the population growth using average fecundity and survival rates for two separate periods: from 1989 to 1994, when the population numbers were relatively high and the population declining, and from 1994 to 1999 when the population size was fairly constant and population numbers low.

Previously estimated survival and fecundity values were used (see Pistorius *et al.* 1999a; Pistorius *et al.* 2001, Chapters 4 & 5) as inputs to the model with initial population sizes equal to the 1989 and 1994 censuses. The predicted instantaneous growth rate was calculated using log-linear regression (Caughley 1977) and compared to the actual growth rates for the two periods, taken from Pistorius *et al.* (1999b) and Chapter 5.

A deterministic model (using Euler's integration in annual time steps) was developed to test the model assumptions and the accuracy of the parameters. This model was calibrated against the actual census data by comparing the slope of the linear regression. An emigration factor had to be added to match the predicted with the actual slope.

An individual-based stochastic population model was subsequently developed, which allowed for demographic and environmental fluctuations and was therefore more realistic. This model assumed that females reproduce during a birth pulse, survive, and are then aged into the next age class. The emigration factor derived from the deterministic model was used in the stochastic model. I imposed variance on survival and fecundity using inter-annual coefficients of variation calculated for the entire period as well as for the two respective periods (declining and stable). I calculated the average growth rate from 1000 replicate simulations.

To measure the sensitivity of population growth to the various vital rates (age-specific survival and fecundity) each parameter was varied by 5% in turn. Survival and fecundity of ages 3 to 5 was also varied by 5% while holding all other parameters constant to explore the effect of changes in survival of prime-age females on population growth (if fecundity was already at the maximum of 0.5 it was not increased). Adult survival was varied by taking the proportion of each age class that was pregnant (from the breeding probability the following year) and altering the survival of the age class by that proportion of 5%. Altering the survival of each age class by the remaining proportion of 5% varied juvenile survival.

Survival was far more important than fecundity in governing changes in population growth (Table 22). Changes in age-specific fecundity of 3- to 5– year-old females mostly had an impact close to an order of magnitude smaller than similar changes in age-specific survival on population growth (Table 22). Over the first five years of life age-specific changes in survival had reasonably similar influences on population growth and this decreased in older animals (Table 22). Population growth rate was more sensitive to changes in adult female survival than changes in juvenile survival. Adult female survival is therefore the most critical parameter affecting population growth and this is in support of the argument that changes in adult female survival have been driving the population decline at Marion Island (Chapter 5). Fecundity appears to be the first to respond to environmental fluctuations (Pistorius *et al.* 2001), and it is therefore important to monitor fecundity for predictive purposes and as an index to environmental change, although it contributes minimally to population status.

Table 24. The percentage change in the average growth rate of 1000 replicates produced by altering one parameter while holding all others constant.

	% change in avg r			*Declining period (1989-1994)*				*Stable period (1994-1999)*				*Entire period (1989-1999)*			
Parameter change	*Decline*	*Stable*	*Entire*	*Avg r*	*Min r*	*Max r*	*St. Dev.*	*Avg r*	*Min r*	*Max r*	*St. Dev.*	*Avg r*	*Min r*	*Max r*	*St. Dev.*
no change				-0.043	-0.084	-0.008	0.0128	-0.002	-0.042	0.047	0.0145	-0.025	-0.061	0.005	0.0100
age 0 survival + 5%	14.53%	284.60%	23.33%	-0.037	-0.076	0.008	0.0123	0.004	-0.041	0.050	0.0140	-0.019	-0.053	0.012	0.0099
age 0 survival - 5%	15.96%	290.05%	24.54%	-0.050	-0.096	-0.012	0.0138	-0.009	-0.052	0.031	0.0146	-0.031	-0.061	0.003	0.0103
age 1 survival + 5%	13.57%	242.24%	20.73%	-0.037	-0.081	-0.004	0.0125	0.003	-0.042	0.052	0.0143	-0.020	-0.048	0.007	0.0100
age 1 survival - 5%	13.55%	282.50%	23.85%	-0.049	-0.084	-0.014	0.0129	-0.009	-0.052	0.033	0.0143	-0.031	-0.062	0.002	0.0106
age 2 survival + 5%	12.82%	253.44%	23.90%	-0.037	-0.084	0.001	0.0128	0.003	-0.047	0.046	0.0140	-0.019	-0.057	0.017	0.0105
age 2 survival - 5%	13.73%	309.99%	25.79%	-0.049	-0.103	0.000	0.0130	-0.009	-0.060	0.039	0.0149	-0.031	-0.068	0.006	0.0107
age 3 survival + 5%	13.16%	235.41%	20.89%	-0.037	-0.084	0.006	0.0129	0.003	-0.042	0.045	0.0141	-0.020	-0.053	0.011	0.0103
age 3 survival - 5%	12.92%	282.55%	22.82%	-0.049	-0.088	-0.005	0.0131	-0.009	-0.062	0.036	0.0151	-0.030	-0.066	0.005	0.0108
age 4 survival + 5%	11.68%	230.19%	19.79%	-0.038	-0.083	-0.005	0.0126	0.003	-0.042	0.050	0.0147	-0.020	-0.049	0.008	0.0099
age 4 survival - 5%	11.56%	197.81%	20.38%	-0.048	-0.087	0.001	0.0131	-0.007	-0.055	0.040	0.0149	-0.030	-0.060	0.008	0.0101
age 5 survival + 5%	7.55%	141.28%	14.41%	-0.040	-0.083	0.004	0.0133	0.001	-0.045	0.039	0.0148	-0.021	-0.050	0.019	0.0100
age 5 survival - 5%	8.87%	191.83%	14.20%	-0.047	-0.101	-0.001	0.0130	-0.007	-0.052	0.034	0.0142	-0.028	-0.068	-0.001	0.0104
age 6> survival + 5%	28.40%	558.44%	52.25%	-0.031	-0.076	0.012	0.0130	0.010	-0.042	0.062	0.0155	-0.012	-0.046	0.023	0.0104
age 6> survival - 5%	26.19%	505.98%	51.17%	-0.054	-0.093	-0.018	0.0121	-0.014	-0.063	0.035	0.0144	-0.037	-0.072	-0.011	0.0099
age 0,1,2 survival + 5%	40.95%	822.97%	69.70%	-0.025	-0.071	0.018	0.0124	0.016	-0.030	0.054	0.0140	-0.007	-0.038	0.020	0.0100
age 0,1,2 survival - 5%	43.31%	771.65%	72.01%	-0.062	-0.108	-0.023	0.0133	-0.019	-0.069	0.029	0.0148	-0.043	-0.076	-0.008	0.0107
age 3,4,5 survival + 5%	33.54%	611.66%	54.96%	-0.029	-0.067	0.007	0.0126	0.011	-0.035	0.049	0.0138	-0.011	-0.045	0.034	0.0100
age 3,4,5 survival - 5%	34.05%	636.20%	56.80%	-0.058	-0.100	-0.013	0.0133	-0.016	-0.061	0.033	0.0150	-0.039	-0.075	-0.008	0.0106
adult survival + 5%	59.57%	1282.39%	108.57%	-0.017	-0.054	0.020	0.0131	0.026	-0.019	0.069	0.0145	0.002	-0.031	0.036	0.0104
adult survival - 5%	58.31%	1267.18%	110.94%	-0.068	-0.108	-0.025	0.0128	-0.031	-0.081	0.012	0.0152	-0.052	-0.083	-0.019	0.0096
juvenile survival + 5%	44.28%	715.60%	68.53%	-0.024	-0.064	0.015	0.0126	0.014	-0.030	0.056	0.0140	-0.008	-0.038	0.025	0.0094
juvenile survival - 5%	45.33%	690.15%	71.25%	-0.063	-0.105	-0.023	0.0135	-0.018	-0.069	0.030	0.0152	-0.042	-0.079	-0.010	0.0107
age 3 fecundity + 5%	0.71%	58.31%	0.40%	-0.043	-0.084	-0.006	0.0129	-0.001	-0.048	0.047	0.0146	-0.025	-0.054	0.002	0.0100
age 3 fecundity - 5%	0.07%	28.99%	2.75%	-0.043	-0.083	-0.003	0.0130	-0.003	-0.052	0.043	0.0143	-0.025	-0.055	0.004	0.0098
age 4 fecundity + 5%	1.22%	-	4.33%	-0.042	-0.086	-0.001	0.0126	-	-	-	-	-0.024	-0.057	0.009	0.0099
age 4 fecundity - 5%	2.03%	31.76%	3.15%	-0.044	-0.085	0.001	0.0125	-0.003	-0.054	0.041	0.0146	-0.026	-0.054	0.008	0.0098
age 5 fecundity + 5%	0.87%	-	1.52%	-0.043	-0.083	-0.001	0.0132	-	-	-	-	-0.024	-0.056	0.010	0.0101
age 5 fecundity - 5%	2.44%	26.06%	2.74%	-0.044	-0.087	-0.001	0.0127	-0.003	-0.053	0.039	0.0145	-0.025	-0.064	0.008	0.0102
age 6> fecundity + 5%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
age 6> fecundity - 5%	7.39%	122.89%	14.98%	-0.046	-0.089	-0.006	0.0130	-0.005	-0.049	0.038	0.0136	-0.028	-0.061	0.010	0.0107
age 3,4,5 fecundity + 5%	5.77%	104.83%	8.71%	-0.041	-0.085	-0.006	0.0127	0.000	-0.052	0.046	0.0149	-0.023	-0.051	0.005	0.0104
age 3,4,5 fecundity - 5%	4.60%	157.23%	9.72%	-0.045	-0.084	-0.003	0.0129	-0.006	-0.058	0.040	0.0147	-0.027	-0.060	0.009	0.0106

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