

PIERRE A PISTORIUS

SURVIVAL OF THE SOUTHERN ELEPHANT SEAL,
MIROUNGA LEONINA, POPULATION OF MARION ISLAND

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**SURVIVAL OF THE SOUTHERN ELEPHANT SEAL,
MIROUNGA LEONINA, POPULATION OF MARION ISLAND**

by

PIERRE A. PISTORIUS

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This thesis is dedicated to the love and lives
of André & Adele Pistorius

“The intricacy of a spider’s web
Man can not hope to understand,
When it lies hidden within the well
Which is being drained with every tree he fells.”

- P.A. Pistorius '97

Survival of the southern elephant seal, *Mirounga leonina*, population of Marion Island

by

Pierre A. Pistorius

Supervisor: Dr. M.N. Bester

Mammal Research Institute

University of Pretoria

Pretoria 0002

South Africa

ABSTRACT

Demographic parameters from a 14 year mark-recapture program on southern elephant seals at Marion Island were investigated. Using the computer package MARK, first year survival was estimated at 0.58 and 0.62, and equated over the first three years of life, 0.69 and 0.74 for males and females respectively. From years four to nine the average survival

rate was 0.66 and 0.75 for males and females respectively. Considerable reductions in fourth and fifth year male survival, and fourth year female survival were observed over the study period. Poor adult survival is implied as the proximate cause, and food limitation as deduced from the decline in survival of seals with high energetic demands, as the ultimate cause behind the population decline. Fecundity was 0.25 for three-year-olds, 0.42 for four-year-olds, and 0.44 for five-year-olds, with a significant increase in these rates being evident over the course of the study. A conversion factor of 3.15 was estimated and applied to annual pup production in order to assess population size. The present population size was estimated at 1263 individuals, and the population declined exponentially at an annual rate of 4.3% from 1986 to 1997, which slowed to 2.5% per annum over the last six years.

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CHAPTER 1 GENERAL INTRODUCTION

1.1 Introduction

A central theme in population ecology embraces the factors that explain changes in population size (Gaillard *et al.* 1998). Variation in survival and fecundity with age and sex directly effects population size (Jorgenson *et al.* 1997). Accurate measures of these parameters are, nevertheless, 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 roles in the dynamics of the population concerned. Long-term studies of population dynamics can be used to identify which vital rates are more variable and which ones are more likely to influence overall changes in population size (Toigo *et al.* 1997).

The population dynamics of southern elephant seal populations has in recent years become an important field of research, due to observed declines in several of these populations (Barrat & Mougin 1978; Condy 1978; Bester 1980; Skinner & Van Aarde 1983; Pascal 1985; Burton 1986; Hindell & Burton 1987; Guinet *et al.* 1992; Bester &

Wilkinson 1994). Although demographic parameters are available for several elephant seal populations (McCann 1985; Hindell 1991; Huber *et al.* 1991; Bester & Wilkinson 1994; Le Boeuf *et al.* 1994), they have often been derived from limited data. Survival parameters are available from the age structure of shot samples (McCann 1985), and from sightings of known-age branded or tagged animals (Hindell 1991; Le Boeuf *et al.* 1994; Bester & Wilkinson 1994). The numbers of individuals in the shot samples were well below that suggested by Caughley (1977) for the determination of an accurate age distribution. The parameters, which are based on life-table analyses, also have assumptions (e.g., random sampling, stability of age structure, and stationary population size over time) that were not necessarily met (see Caughley 1977; Seber 1982). The general problems with survival estimates obtained from resightings of marked individuals have been the use of single cohorts with a limiting number of recapture years (Wilkinson 1991) and inconsistent search effort (Hindell 1991).

A study performed by Wilkinson (1991) suggested that the elephant seal population at Marion Island declined at a rate of 4.8% per annum over the period 1951 to 1989, which slowed to 1.9% per annum over the period 1983 to 1989. The driving force(s) behind the elephant seal population decline at Marion Island, as well as declines over other parts of their range, are poorly understood. Several hypotheses regarding the decline have been discussed by Hindell *et al.* (1994) (see also Hindell 1991).

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 have 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; Carrick *et al.* 1962a), social maturity is only attained at about eight years of age (Laws 1984; S.P. Kirkman unpublished results). All females are recruited into the adult population at age six (Wilkinson 1991). A longevity of 20 and 23 years have been recorded for males and females respectively (McCann 1985; Hindell & Little 1988).

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 are 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 spend approximately eight months and females 10 months a year at sea, 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 1991; 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, who gradually congregate in harems and reach a maximum number on the 15th of October (Condy 1979; Wilkinson 1991). 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 1991). Mating takes place approximately 18 days after parturition and the dominant males obtain over 98% of the matings (Wilkinson 1991). Assistant beachmasters are not often encountered on Marion Island due to the relatively small harems (Wilkinson 1991). 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 1956b; King 1983).

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. 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 & Arnborn 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 outer edge of 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, 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,



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).

Campbell Island, Auckland Islands, and Antipodes Islands. Recent genetic studies suggested that the Falkland Islands and South America 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 Valdes accounted for 60%, Iles Kerguelen 28%, and Macquarie Island 12% (Laws 1994). The South Georgia population appears to have been almost stable since 1951 (Laws 1960; McCann & Rothery 1988; Laws 1994) but both the Iles Kerguelen and Macquarie Island stocks declined steadily over forty years from at least 1950 (Van Aarde 1980; Hindell & Burton 1987; Guinet *et al.* 1992), although the Iles Kerguelen population has recently been thought to have stabilised (Guinet *et al.* 1992). The Marion Island population decreased by 83.7% between 1951 and 1990 and in percentage terms, have been the most adversely affected of all except those at Signy Island and Campbell Island (Condy 1978; Bester & Wilkinson 1994; Laws 1994).

1.4 Objectives of the Study

The objectives of this study can be divided into four sections, and these are presented as separate chapters. The aims of the first section (chapter 3) were to provide factors to correct for tag loss in estimates of survival of southern elephant seals, to quantify the effectiveness of Dalton Jumbo Rototags for marking elephant seals, and to demonstrate an adaptation of a new method for estimating tag loss. The aims of the following sections were to assess age-specific survival for both sexes (chapter 4), and age-specific fecundity rates (chapter 5) for the elephant seal cohorts 1983-1992 at Marion Island, in which

marked animals were consistently monitored for a period of 14 years. Recently developed capture-mark-recapture models were used for this purpose. Attempts were also made to observe changes in these demographic parameters over the extent of the study period during which the population was in a state of decline. The determination of these parameters permitted the identification of the stages that contributed most prominently towards the population decline, and this allowed speculation as to the ultimate factor driving the decline. The fourth section (chapter 6) aimed at determining the present population size and rate of population change, as well as providing a standing age-distribution for the southern elephant seal population at Marion Island.

The importance of this study is signified by the paucity of long term demographic data for mammals. In order to understand the processes responsible for changes in population parameters requires the acquisition of such long term data. Besides it being integral to an understanding of the population decline at Marion Island, these parameters can be used as an index of change in other components of the southern ocean in the region of Marion Island, as well as being useful as a management tool.

CHAPTER 2 STUDY AREA

2.1 Location

Marion Island ($46^{\circ}54'S$, $37^{\circ}45'E$) 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 72 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

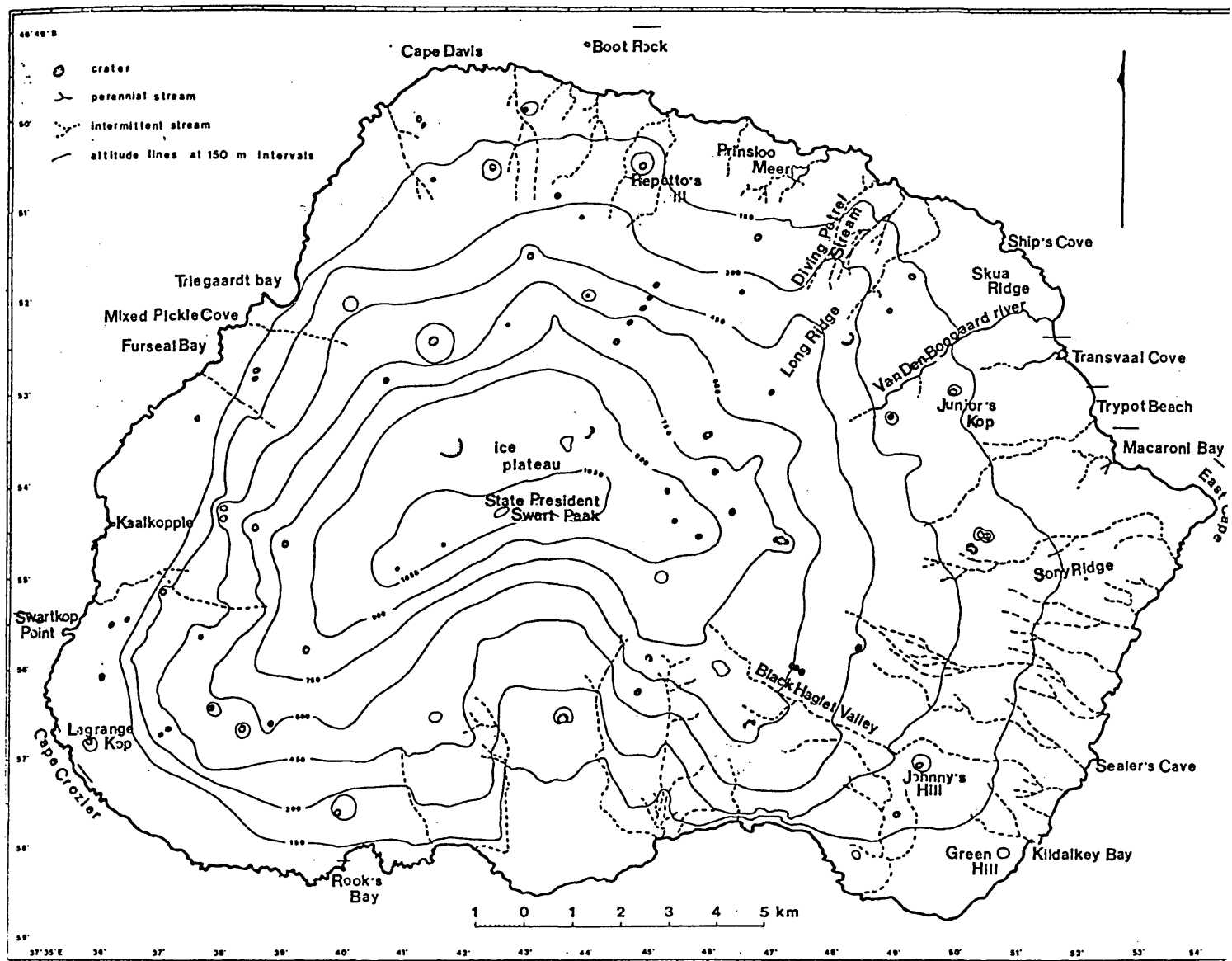


Figure 2. Topographical map of Marion Island (taken from Gremmen 1981).

distinct 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 coast-line 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 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 AGE-DEPENDENT RATES OF TAG LOSS

3.1 Introduction

The tagging of pinnipeds facilitates studies of their life history, demography, behaviour, growth and development, dispersal, and fidelity to birth or breeding sites. The propensity for tags to be lost, however, requires consideration of the rate of tag loss in these studies (e.g., Arnason & Mills 1981). Ideally, some permanent mark would be applied in conjunction with tags to allow not only estimation of the rate of tag loss, but also assessment of whether tag loss is independent in studies that utilise double tagging (Diefenbach & Alt 1998). However, the addition of a permanent mark is not always practical in pinniped studies. Also, some types of permanent marks such as lip tattoos (Diefenbach & Alt 1998) lend themselves well to mark-recapture designs but not to the tag-resight design that is often used for pinnipeds, because the free-ranging tagged animals cannot typically be inspected closely enough to detect such marks. To estimate tag loss in tag-resight studies without permanent marks, it is usually necessary to use double, identical tags and assume that loss of each tag is independent of the other.

In this study, double tagging without permanent marks were used to investigate the rates of tag loss in 11 cohorts of southern elephant seals at Marion Island. The aims of the study were to provide factors to correct for tag loss in estimates of survival of southern elephant seals, to quantify the effectiveness of Dalton Jumbo Rototags® for marking elephant seals, and to demonstrate an adaptation of a new method for estimating tag loss (Barrowman & Myers 1996) that was originally developed for a mark-recapture study of fish.

3.2 Methods

3.2.1 Tagging and resighting of seals

From 1983 to 1993, southern elephant seal pups were double tagged in their hind flippers just after weaning on Marion Island (Table 1; Fig. 3). The tags were Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley on Thames, United Kingdom), which had a higher retention rate than other cattle ear tags in a study on Weddell seals (Testa & Rothery 1992). The self-piercing tags were uniquely numbered with three digits and colour coded to denote the year of application (Fig. 4). Tags used in 1983-1986 consisted of two components, one bearing the tag number and the other the tagging site (Marion Is). Tags used since 1987 had the number printed on the outside and the tagging site printed on the inside of each part. The tags were inserted in the centre of either of the inner two sections of interdigital webbing of each hind flipper, so that approximately one third of the length of the tag



Figure 3. The tagging of a recently weaned southern elephant seal at Marion Island.



Figure 4. The hind flipper of a tagged adult male elephant seal.

extended beyond the edge of the webbing. The sex and the birth site (specific beach) of the pup were recorded at the time of tagging.

From 1983 to 1998, beaches were searched for tagged seals every seven days during the breeding season (mid-August to mid-November), every 10 days during the moulting period (mid-November to mid-April) and, since 1990, every 10 days during the winter (mid-April to mid-August). The reason for the more frequent visits during the breeding season was the increased difficulty of resighting and reading tags in harems, compared to the moulting seasons when seals were more widely dispersed. The tag number, colour, and number of tags were recorded for each resight used in this study.

Because multiple resights of individual seals within a particular year provide relatively little information about age-specific tag loss (compared with resights of individuals over the course of several years), the data set was reduced to include only the last resight of each seal in each research season.

3.2.2 Estimation of tag loss

Rates of tag loss were estimated by a maximum likelihood method (Barrowman & Myers 1996) based on the time at liberty of seals that were double-tagged shortly after weaning. Although the method was developed for situations where tagged animals are released and then recaptured (removed from the population), it was adapted to a “mark-resight” situation by considering a resight to be a recapture followed by another release. The likelihood function was composed of the relative probabilities that a seal tagged or sighted

previously with two tags would have one or two tags remaining when resighted at some later time.

It was assumed that the instantaneous rate of loss of a single tag, denoted μ , is a linear function of a , the age of the tagged seal, $\mu(a) = \beta_1 + \beta_2 a$, where β_1 is an age-constant component of tag loss and β_2 is an age-dependent component of tag loss. Then the probability of retaining a tag for some time interval t (i.e., from age a to age $a + t$) is

$$Q(a, a + t) = e^{-\int_a^{a+t} \mu(x) dx} = e^{-\beta_1 t - \beta_2 a t - \frac{1}{2} \beta_2 t^2}$$

Note that this formula encompasses two hierarchical models that can be tested for the best fit to the data; an age-constant model with $\beta_1 > 0$ and $\beta_2 = 0$, and an age-independent model with $\beta_1 > 0$ and $\beta_2 \neq 0$.

Some tags may be lost shortly after tagging for various reasons (e.g., poor tag placement, infection of the tagging site) that are different from the primary causes of long-term tag loss (e.g., fatigue and failure of the tag itself, gradual enlargement of the tag hole). Therefore, a term was added to the model for the probability of losing a tag immediately after tagging (Barrowman & Myers 1996). A simple way to incorporate this term into the model notation (Barrowman & Myers 1996) is to consider a tag to be of type A until it is first resighted and of type B thereafter. Thus, a seal was considered to have been tagged initially as AA , and each subsequent resight was considered to be a recapture as AA or A ,

followed by a release as BB or B , if it had two tags or one tag, respectively. Then the probability that a tag is retained at time t after the initial release is,

$$Q_A(0, t) = \beta_0 e^{-\beta_1 t - \frac{1}{2} \beta_2 t^2},$$

where β_0 is the probability of retaining a tag immediately after tagging, and the probability that the tag is retained for t time units after a seal was resighted with the tag at age a ($a \neq 0$) is

$$Q_B(a, a+t) = e^{-\beta_1 t - \beta_2 a t - \frac{1}{2} \beta_2 t^2}.$$

Again following the notation of Barrowman & Myers (1996), let $p_y^x(a, a+t)$ be the probability of observing tag combination y on a seal t time units after the seal was released (or resighted) at age a with tag combination x . Note that this probability and all others associated with resighting are conditional on the seal having been resighted at time t . For example, $p_{AA}^{AA}(0, t)$ is the probability, conditional on the seal having been resighted, that a seal that was double tagged initially retained both tags when sighted at time t . Then, assuming independence of tag loss between the two tags on a seal, the probabilities of all the various outcomes following releases of seals double-tagged AA , and “releases” (resights) of seals double-tagged BB are,

$$p_{AA}^{AA}(0, t) = Q_A(0, t)^2,$$

$$p_A^{AA}(0, t) = 2Q_A(0, t)[1 - Q_A(0, t)],$$

$$p_{BB}^{BB}(a, a+t) = Q_B(a, a+t)^2, \text{ and}$$

$$p_B^{BB}(a, a+t) = 2Q_B(a, a+t)[1 - Q_B(a, a+t)].$$

An index was assigned $i = 1, 2, 3,$ and $4,$ respectively to these outcomes and let n_i be number of times outcome i occurred in the resighting data. Then, letting t_{ij} represent the combination of seal age and resighting time of the j^{th} observation of outcome $i,$ the log likelihood for the data, conditional on the resighting times is,

$$l = \sum_{j=1}^{n_1} \log \left(\frac{P_1(t_{1j})}{P_1(t_{1j}) + P_2(t_{1j})} \right) + \sum_{j=1}^{n_2} \log \left(\frac{P_2(t_{2j})}{P_1(t_{2j}) + P_2(t_{2j})} \right) + \sum_{j=1}^{n_3} \log \left(\frac{P_3(t_{3j})}{P_3(t_{3j}) + P_4(t_{3j})} \right) + \sum_{j=1}^{n_4} \log \left(\frac{P_4(t_{4j})}{P_3(t_{4j}) + P_4(t_{4j})} \right).$$

The log likelihood was maximised over values of $\beta_0, \beta_1,$ and β_2 using the downhill simplex method (Nelder & Mead 1965; Press *et al.* 1992). The probability of initial tag retention, $\beta_0,$ was constrained to values between zero and one during the maximisation by a trigonometric transformation. The age-constant portion of the instantaneous rate of tag loss, $\beta_1,$ was constrained to positive values by a logarithmic transformation. The age-constant model was fit by holding $\beta_2 = 0.$ The age-constant and age-independent models were compared by Akaike's information criterion (AIC) which is $2l - 2r,$ where r is the number of parameters estimated (Akaike 1974); a difference in AIC of greater than two was considered to represent a significant difference between models. Both the age-constant and age-independent models were fit separately for resights of males and females, as well as to the pooled resights of males, females, and seals of unknown sex.

To apply this method of estimation of tag loss, the following additional assumptions were made:

1. The “reporting rate” is 1.0 for all seals that retain at least one tag. In other words, if a seal had at least one tag and was in the seal colony where resights took place, it would be resighted with certainty. A known or independently estimated value for reporting rate could easily be incorporated into the likelihood model (Barrowman & Myers 1996).
2. All seals were born on 15 October, the date of peak haulout for breeding females (Wilkinson 1991) and tagged on 15 November of the cohort year.
3. The rate of tag loss did not vary with cohort-specific aspects such as seal condition or the persons applying the tags.

Probabilities of tag retention were estimated using methods described in Arnason & Mills (1981).

3.3 Results

For both the age-constant and age-dependent models of tag loss, the initial probability of retaining a tag, β_0 , was estimated to be 0.998 regardless of whether the model was fit to data from males, females, or all seals combined. Therefore, to increase the precision of estimating the other parameters, β_0 was held fixed at 0.998 for all the results presented hereafter. When the data for all seals combined were fit to the age-constant model, the

instantaneous rate of tag loss was estimated to be 0.02 (Table 2), translating to a 2% probability of losing a particular tag per year, regardless of age. However, AIC for the age-dependent model was lower by 59 than AIC for the age-constant model, indicating that the age-dependent model provided a much better fit to these data. The values for β_1 and β_2 (Table 2), indicated that the instantaneous rate of tag loss increased from 0.010 at birth to 0.072 at age 14. The age-constant model, therefore, overestimated the rate of tag loss for young seals and underestimated it for older seals.

The dependence of tag loss on age was supported by the separate analyses of resighting times of male and female seals (Table 2). However, the increase in the rate of tag loss with age was much stronger for males ($\beta_2 = 0.007$), than for females ($\beta_2 = 0.003$). Therefore, even though the age-constant portion of instantaneous tag loss appeared greater for females ($\beta_1 = 0.012$) than for males ($\beta_1 = 0.007$), the total instantaneous rate ($\beta_1 + \beta_2 \cdot \text{age}$) for males surpassed that for females by age three years and was nearly double the rate for females by age 14 years.

The age and sex differences in the instantaneous rates of tag loss are perhaps mostly easily interpreted in terms of annual probabilities of tag loss (Table 3). For both males and females, the probability of losing a particular (single) tag during the first year of life was only about 1%. This probability increased to 10% for males and 5% for females during the interval from 14 to 15 years of age. The cumulative probabilities, from birth to age 15, of double-tag loss were 35% for males and 16% for females. Tag retention rates, which were applied to the survival estimates in chapter four in order to correct for the bias resulting from tag loss, are presented in tables 4 and 5 for males and females respectively.

Table 1. Numbers of recently-weaned southern elephant seals tagged annually at Marion Island.

Year	Male	Female	Sex unknown	Total
1983	209	198	9	416
1984	260	234	4	498
1985	357	343	0	700
1986	280	278	5	563
1987	296	312	1	609
1988	296	285	1	582
1989	241	267	7	515
1990	239	249	1	489
1991	223	245	1	469
1992	222	224	5	451
1993	243	208	0	451
Total	2866	2843	34	5743

Table 2. Estimates from two models for the instantaneous rate of tag loss. In the constant model, the instantaneous rate of tag loss is β_1 . In the age-dependant model, the instantaneous rate of tag loss is $\beta_1 + \beta_2 a$, where a is the age of the seal in years. Models were compared by Akaike's information criterion (AIC); a difference in AIC of more than 2 indicates a significant difference between models fit to the same data.

Sex	Model	β_1 (s.e.)	β_2 (s.e.)	AIC
Male + Female + Unknown	constant	0.0206 (0.0010)		3703
Male + Female + Unknown	age-dependent	0.0098 (0.0016)	0.0044 (0.0007)	3644
Male	constant	0.0221 (0.0016)		1749
Male	age-dependent	0.0067 (0.0025)	0.0070 (0.0011)	1697
Female	constant	0.0194 (0.0013)		1937
Female	age-dependent	0.0116 (0.0021)	0.0030 (0.0008)	1918

Table 3. Probabilities of tag loss estimated for southern elephant seals at Marion Island, using an age-dependant model. The probabilities of losing an individual tag are shown as age-specific values. The probabilities of losing both tags are shown as cumulative values from birth to the end of the age interval.

Age	<u>MALES</u>		<u>FEMALES</u>	
	Age-specific single tag loss	Age-cumulative double tag loss	Age-specific single tag loss	Age-cumulative double tag loss
0 – 1	0.0122	0.0001	0.0150	0.0002
1 – 2	0.0171	0.0008	0.0159	0.0009
2 – 3	0.0239	0.0027	0.0189	0.0024
3 – 4	0.0307	0.0066	0.0218	0.0049
4 – 5	0.0374	0.0134	0.0247	0.0086
5 – 6	0.0441	0.0239	0.0276	0.0138
6 – 7	0.0507	0.0390	0.0305	0.0209
7 – 8	0.0573	0.0593	0.0334	0.0300
8 – 9	0.0638	0.0851	0.0362	0.0412
9 – 10	0.0703	0.1167	0.0391	0.0549
10 – 11	0.0768	0.1538	0.0420	0.0709
11 – 12	0.0832	0.1960	0.0448	0.0895
12 – 13	0.0896	0.2427	0.0476	0.1106
13 – 14	0.0959	0.2930	0.0505	0.1342
14 – 15	0.1022	0.3459	0.0533	0.1600

Table 4. Probabilities of tag retention and loss for southern elephant seal males at Marion Island, based on resights of the cohorts tagged in 1983-1993.

Age	<u>SINGLE TAG PROBABILITIES</u>				<u>DOUBLE TAG PROBABILITIES</u>			
	Age-specific retention loss		Cumulative retention loss		Age-specific ret. 1 or 2 loss		Cumulative ret. 1 or 2 loss	
0	0.9878	0.0122	0.9878	0.0122	0.9999	0.0001	0.9999	0.0001
1	0.9829	0.0171	0.9710	0.0290	0.9993	0.0007	0.9992	0.0008
2	0.9761	0.0239	0.9478	0.0522	0.9981	0.0019	0.9973	0.0027
3	0.9693	0.0307	0.9188	0.0812	0.9961	0.0039	0.9934	0.0066
4	0.9626	0.0374	0.8844	0.1156	0.9932	0.0068	0.9866	0.0134
5	0.9559	0.0441	0.8454	0.1546	0.9893	0.0107	0.9761	0.0239
6	0.9493	0.0507	0.8026	0.1974	0.9845	0.0155	0.9610	0.0390
7	0.9427	0.0573	0.7566	0.2434	0.9789	0.0211	0.9407	0.0593
8	0.9362	0.0638	0.7083	0.2917	0.9725	0.0275	0.9149	0.0851
9	0.9297	0.0703	0.6584	0.3416	0.9655	0.0345	0.8833	0.1167
10	0.9232	0.0768	0.6079	0.3921	0.9580	0.0420	0.8462	0.1538
11	0.9168	0.0832	0.5573	0.4427	0.9501	0.0499	0.8040	0.1960
12	0.9104	0.0896	0.5074	0.4926	0.9419	0.0581	0.7573	0.2427
13	0.9041	0.0959	0.4587	0.5413	0.9336	0.0664	0.7070	0.2930
14	0.8978	0.1022	0.4118	0.5882	0.9251	0.0749	0.6541	0.3459

Table 5. Probabilities of tag retention and loss for southern elephant seal females at Marion Island, based on resights of the cohorts tagged in 1983-1993.

Age	<u>SINGLE TAG PROBABILITIES</u>				<u>DOUBLE TAG PROBABILITIES</u>			
	Age-specific retention loss		Cumulative retention loss		Age-specific ret. 1 or 2 loss		Cumulative ret. 1 or 2 loss	
0	0.9850	0.0150	0.9850	0.0150	0.9998	0.0002	0.9998	0.0002
1	0.9841	0.0159	0.9693	0.0307	0.9993	0.0007	0.9991	0.0009
2	0.9811	0.0189	0.9510	0.0490	0.9985	0.0015	0.9976	0.0024
3	0.9782	0.0218	0.9303	0.0697	0.9975	0.0025	0.9951	0.0049
4	0.9753	0.0247	0.9074	0.0926	0.9963	0.0037	0.9914	0.0086
5	0.9724	0.0276	0.8823	0.1177	0.9947	0.0053	0.9862	0.0138
6	0.9695	0.0305	0.8554	0.1446	0.9928	0.0072	0.9791	0.0209
7	0.9666	0.0334	0.8269	0.1731	0.9907	0.0093	0.9700	0.0300
8	0.9638	0.0362	0.7969	0.2031	0.9884	0.0116	0.9588	0.0412
9	0.9609	0.0391	0.7658	0.2342	0.9858	0.0142	0.9451	0.0549
10	0.9580	0.0420	0.7337	0.2663	0.9830	0.0170	0.9291	0.0709
11	0.9552	0.0448	0.7008	0.2992	0.9800	0.0200	0.9105	0.0895
12	0.9524	0.0476	0.6674	0.3326	0.9768	0.0232	0.8894	0.1106
13	0.9495	0.0505	0.6337	0.3663	0.9735	0.0265	0.8658	0.1342
14	0.9467	0.0533	0.5999	0.4001	0.9701	0.0299	0.8400	0.1600

3.4 Discussion

3.4.1 Effects of age and sex on tag loss

At an earlier stage of this study, Wilkinson & Bester (1997) found no significant effect of age or sex on rates of tag loss, but they speculated that with larger samples and longer duration of the study, tag loss would be shown to increase with age and more strongly for males than females. The present results are entirely consistent with their speculation. The most likely explanation for the stronger increase in rate of tag loss with age for males is, as Wilkinson & Bester (1997) proposed, that the more rapid growth and much larger size of males causes their flippers to thicken more rapidly to the point of interfering with the well-being of the tag and its placement site.

The general aspect of tag loss increasing with age may be a result of effects related to increasing age of the seal, increasing age of the tag itself, or both. Because the seals in our study were tagged at approximately one month of age, seal age and tag age were nearly identical. However, these effects can be tested separately in studies where some seals are tagged at birth and others are tagged later, at known ages (approximate age may be sufficient) (e.g., Testa & Rothery 1992).

Although little evidence was found for a period of higher tag loss immediately following tagging ($\beta_0 = 0.998$), it is a good idea to include this term in the model when applying our method to other species or situations. The relatively high rate of first-year tag loss observed in Weddell seals (*Leptonychotes weddellii*) (Croxall & Hiby 1983; Testa &

Siniff 1987; Testa & Rothery 1992) may be evidence for tag loss from initial effects of tagging, such as failure of the wound to heal or occasional miss-applied tags.

3.4.2 Choice of analytical method

Tag loss in double-tagging studies of pinnipeds (Testa & Rothery 1992; Shaughnessy 1994; Stobo & Horne 1994; Boyd *et al.* 1995; Wilkinson & Bester 1997) has usually been estimated by the method presented by Chapman *et al.* (1965) and Eberhardt *et al.* (1979). In that method, the probability of losing an individual tag during some time interval is $n_1/(n_1 + 2n_2)$, where n_1 and n_2 are the numbers of animals recovered at the end of the interval retaining one and two tags, respectively, having been double-tagged at the beginning of the interval. Because this method was derived in consideration of mark-recapture techniques, in which animals are usually marked, left at liberty for some time, and then recaptured (perhaps in a harvest), it can be difficult to apply correctly to a mark-resight study in which marked animals remain at liberty and are resighted, perhaps at various times throughout the year and multiple times during the study. Care must be taken to include in a single estimate only those animals that have been at liberty for the same amount of time; it may even be necessary to discard data from animals absent for a year or more between resights, making for inefficient use of the data. The estimates may be biased and lack independence if multiple resights of an individual seal are used to estimate the cumulative probabilities of tag loss from birth to several different ages, without accounting for the conditional nature of the probability of retaining a tag from one resight to the next. Finally, because this estimator is a ratio of numbers of recoveries or resights, which will

almost always be small numbers for the older animals, estimates of age-specific tag loss typically become highly variable and unstable, with values tending to be either zero or one for the oldest age classes.

The maximum likelihood method used in this study (Barrowman & Myers 1996) overcomes these problems associated with the ratio method. It uses the exact time at liberty for each resight so all resights can be included in the estimate, regardless of whether resights are obtained throughout the year and regardless of the amount of time since tagging or the most recent resight. Provided that a resight is treated as a recapture and subsequent release, the likelihood method accounts correctly for the conditional probabilities associated with multiple resights of the same animal. The method allows estimation of the effects of age (or other co-variates) on tag loss by modelling the effects with a relatively small number of parameters, thus avoiding the instability that results from estimating age-specific tag loss separately for each age by the ratio method. Incorporating co-variates directly into the likelihood is an alternative—though not necessarily superior—to the categorical analysis approach taken by Testa & Rothery (1992) and the logistic regression approach taken by Stobo & Horne (1994). Finally, the likelihood method provides a natural framework for estimation of tag loss when more than one tag type has been used in a study (Testa & Rothery 1992; Barrowman & Myers 1996).

CHAPTER 4 SURVIVAL IN RELATION TO AGE, SEX & COHORT

4.1 Introduction

Fundamental to the study of animal population biology is an understanding of the animal's population dynamics (Lebreton *et al.* 1993). The study of population dynamics, and hence life history parameters, is becoming increasingly important in the field of ecology and a major objective is to detect and analyze differences in life history traits among groups of individuals through space and time (Lebreton *et al.* 1992). These differences often induce changes in survival and fecundity, which in turn govern rates of population change (Bowen *et al.* 1981).

As is the case with several other southern elephant seal populations, the Marion Island population has declined over the past few decades (Barrat & Mougín 1978; Condy 1978; Bester 1980; Skinner & Van Aarde 1983; Pascal 1985; Burton 1986; Hindell & Burton 1987; Guinet *et al.* 1992; Bester & Wilkinson 1994), with no single cause being unequivocally identified. Birth, death, immigration and emigration are the four fundamental demographic parameters that influence the survival of a population (Brewer 1994). While the foraging ranges of several elephant seal populations overlap, there

appears to be very limited immigration and emigration between the different populations as a consequence of the high level of philopatry which is characteristic of this species (Hindell & Little 1988; Bester 1989). The decline of the Marion Island population is therefore a result of mortality rate exceeding birth rate.

The most reliable method of determining age-specific survival and fecundity is to follow the fate of a group of individuals, all born during the same time interval (Begon & Mortimer 1986). Long-term monitoring is required in order to yield the necessary data to test for age-, sex- and time-dependent effects on survivorship. A comprehensive elephant seal tagging programme commenced at Marion Island in 1983, rendering consistent long-term recapture data. The aim of this chapter was to assess age- and sex-specific survival rates in 10 cohorts of southern elephant seals. This was done in order to investigate possible proximate causes of the observed population decline, which would permit speculation as to the ultimate cause.

Survival parameters are available for the declining Macquarie Island and Marion Island populations (Hindell 1991; Wilkinson 1991; McMahon *et al.* 1999), the stable South Georgia and Falkland Islands populations (McCann 1985; Galimberti & Boitani 1999), and the increasing northern elephant seal population at Año Nuevo, California (Le Boeuf *et al.* 1994). Several branded cohorts of weaned pups at Macquarie Island were followed over their entire lifespan (Hindell 1991; McMahon *et al.* 1999) and survival estimates were based on the minimum number of individuals alive at each age (Hindell 1991), whereas survival data for the South Georgia population were based on the age structure of shot

samples. The results from these studies have made some comparison between populations possible.

4.2 Methods

Mark-recapture methods are widely used to obtain data for estimations of the various parameters of animal populations, where these data consist of a record of the captures and recaptures of marked animals obtained over a period of time (Manly 1970; Begon & Mortimer 1986; Lebreton *et al.* 1992). Between 1983 and 1997, a total of 7391 (average: 499 tagged annually; range: 394-700) of recently weaned elephant seal pups were double tagged at Marion Island, with uniquely numbered, colour coded Dal 008 Jumbotags (chapter three). Date, location and pup sex were recorded at the time of tagging. All the study beaches (32 along a 51.9km coast line) were checked weekly during the breeding season (mid-August to mid-November), and every ten days outside of the breeding season, for tagged elephant seals except prior to 1990, when no censuses were conducted during the winter months (June, July and August). The reason for the more frequent censuses during the breeding season was related to the increased difficulty of reading tags in harems. All seals were assumed to age on 15 October, which is the peak haul-out date for adult females on all the Indian Ocean breeding sites (Condy 1978; Bester & Wilkinson 1994). 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), location and date of sighting. The data was entered into the DBASE IV (Ashton Tate) software package for future analysis. Where possible, tags were read without physical contact to minimize

disturbance, but when necessary the hind flippers were spread. All the beaches that are regularly frequented by elephant seals are accessible on foot. When individuals hauled out onto inaccessible beaches, attempts were made to read the tags with binoculars from the cliff-tops.

Capture-history matrices were constructed using the recapture data from the 1983-1992 cohorts, treating multiple sightings within a year as a single sighting. Fourteen years of capture history was available for the 1983 cohort and five years for the 1992 cohort. These matrices were used as input files for the computer software package MARK (G White, University of Colorado), designed to obtain maximum likelihood estimates of survival and capture probability rates from the resighting of marked individuals. 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 i^{th} and $(i+1)^{\text{th}}$ sample
($i=1, \dots, k-1$), and

p = the capture probability for all animals in the i^{th} sample ($i=1, \dots, k$).

Goodness-of-fit tests of the CJS model, which is a full time-dependant model, were performed in order to check the assumptions pertaining to the model using the RELEASE

program (Burnham *et al.* 1987). As age-dependence was assumed, and the different cohorts were treated separately, Test 3.Sm was retained (see Lebreton *et al.* 1992).

The CJS model is often criticised as being too general, due to the fact that separate parameters are included for each survival and capture probability (Cormack 1979; Pollock *et al.* 1990). The models that appear as special cases of this model are generally referred to as constrained models, the constraints mostly involving equality between parameters. If a reduction in parameters is justified by the data, it results in a more accurate estimation of the remaining parameters (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 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). This method 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. Survival rates in large mammals are expected to plateau as animals achieve adult status (Caughley 1977). All the females at Marion Island are recruited into the adult population at six years of age (Wilkinson 1991). Although puberty in southern elephant seal males is reached between about four and six years of age (Laws 1956a; Carrick *et al.* 1962a), social maturity is only attained at about eight years of age (Laws 1984; S.P. Kirkman unpublished results). Survival probabilities were therefore

maintained constant from ages eight and six onwards for males and females respectively, and if this reduced the AIC value further, the model was selected.

Age-specific tag retention rates, estimated from double-tagged individuals (chapter three), were used to adjust the survival estimates to compensate for tag loss.

The probability of surviving to a given age (l_x) was calculated from the product of all the survival values (ϕ) prior to that age. A life table was drawn up, for males and for females, using survival data (ϕ) averaged across the cohorts 1983-1992. This yielded a general representation of the survival schedule for the elephant seal population at Marion Island, as well as reducing the possible effects of short term environmental and demographic stochasticity on the survival estimates. It is important to differentiate between cohort and stationary life tables (Caughley 1977; Krebs 1985). The cohort life table (above) provides the proportion of individuals surviving to each age, whereas the stationary life table provides the proportion of animals, relative to the number of new born, in each age class at a particular time.

The l_x values were used to determine the probability of dying ($d_x = l_x - l_{x+1}$), and mortality rate ($q_x = d_x/l_x$), whereas survival rates were taken from the MARK survival estimates ($\phi = p_x$).

Age-specific survival estimates from the ten consecutive cohorts were plotted against each other, firstly to illustrate inter-annual changes in survival estimates, and secondly in an effort to identify years of poor survival. Attempts were made to identify

linear trends in survival using Pearson's linear regression. The Kolmogorov-Smirnov test was used to test the data for deviations from a Gaussian distribution. The cohorts for which comparable age-specific survival estimates were available, were separated into two groups, to relate estimate means of the earlier (mostly 1983-1987) and later periods (mostly 1988-1992). The median value was included into both periods in cases where means were calculated using uneven numbers of estimates.

4.3 Results

Table 6 shows the results of the GOF tests (program RELEASE) for males and females separately for each cohort. Three out of the 20 data sets showed departures from the CJS model (1986, 1987 and 1990 males), and results from these data sets should be interpreted with relative caution.

The constant capture probability model was selected for the majority of cohorts, and in several cases adult survival was maintained constant (Table 7). Survival estimates with standard errors, and capture probability estimates are presented in tables 8-18. Cohort life tables were constructed from the age-specific survival estimates averaged over the 1983-1992 cohorts, for males and for females, and are presented in Tables 19 & 20. Survivorship curves for males and females are given in Fig.5.

The most conspicuous peak in mortality for both sexes occurred in the first year of life. There were subsequent peaks in the fourth and ninth year mortality among males. Although a 100% mortality is observed in the 13th year, this is an artefact of the very small

sample size. After year one, relatively high mortality rates were evident among two-, five- and eight-year-old females. Nevertheless, females in their second to eighth year, had rather similar mortality rates, with a range of only 7.9%.

Mortality rates were higher among males than among females in all the age-classes (Tables 19 & 20). The most remarkable sexual differences in mortality were found for ages three, eight, nine and 10.

Because inter-cohort age-specific survival estimates were normally distributed ($p > 0.10$ in all cases), it was not necessary to transform the data before performing linear regression analysis. No significant deviations from slope zero were evidenced by F-tests in any of the data sets (Figs 6-13). Although not statistically significant, a negative trend was observed when fitting a regression line to the survival estimates of males in their fourth year. Adjacent estimates of fourth year survival were subsequently grouped and analysed using linear regression. There was a distinct negative linear trend in survival (slope = -0.046 ± 0.009 , $r^2 = 0.984$, $p = 0.001$). A reduction in survival was visible for several age classes when comparing the averages of the age-specific survival estimates from the earlier (mostly 1983-1987 cohorts) and later (mostly 1988-1992 cohorts) periods (Table 21). The decrease in survival of three- and four-year-old males is particularly noteworthy. Among females, three-year-olds experienced the most severe reduction in survival.

The high mortality of three-year-old females in the 1983 cohort (Table 9, Fig. 9) corresponds to a high mortality of two-year-old females in the 1984 cohort (Table 10, Fig. 8). Both these groups therefore experienced high mortalities in 1987. This further

Table 6. Goodness-of-fit tests of the Cormack-Jolly-Seber model by southern elephant seal cohort.

Cohort	<u>MALES</u>			<u>FEMALES</u>		
	χ^2	df	P	χ^2	df	P
1983	8.37	3	0.039	1.32	3	0.724
1984	1.79	4	0.774	3.61	1	0.058
1985	6.25	2	0.044	8.51	5	0.130
1986	12.08	3	0.007	9.90	4	0.042
1987	12.51	1	0.001	6.35	2	0.042
1988	0.301	3	0.960	7.66	4	0.105
1989	0.001	2	0.999	1.09	3	0.780
1990	7.225	1	0.007	1.23	2	0.540
1991	0.001	1	0.999	4.88	2	0.087
1992	0.001	1	0.999	1.24	1	0.027

Table 7. Elimination of nonsignificant effects from the full CJS model in modeling survival in southern elephant seals at Marion Island: for each model the number of estimable parameters (np), the deviance (DEV), and the Akaike information criterion (AIC) are given. The bold AIC value represents the selected model.

Cohort	Model	<u>MALES</u>			Model	<u>FEMALES</u>		
		np	DEV	AIC		np	DEV	AIC
1983	(1) (ϕ_t, p_t)	24	213.60	1207.74	(ϕ_t, p_t)	24	228.28	1287.28
	(2) (ϕ_t, p_c)	12	224.61	1201.65	(ϕ_t, p_c)	14	243.49	1281.20
	(3) (ϕ_{1-9}, p_c)	10	232.66	1205.52	(ϕ_{1-7}, p_c)	8	250.76	1275.95
1984	(1) (ϕ_t, p_t)	23	144.16	1187.62	(ϕ_t, p_t)	23	277.55	1370.52
	(2) (ϕ_t, p_c)	13	162.80	1184.81	(ϕ_t, p_c)	13	291.63	1363.39
	(3) (ϕ_{1-9}, p_c)	10	164.55	1180.29	(ϕ_{1-7}, p_c)	8	297.39	1358.79
1985	(1) (ϕ_t, p_t)	21	267.67	1931.19	(ϕ_t, p_t)	21	363.63	2182.07
	(2) (ϕ_t, p_c)	12	280.09	1924.87	(ϕ_t, p_c)	12	395.59	2195.33
	(3) (ϕ_{1-9}, p_c)	10	280.19	1920.87	(ϕ_{1-7}, p_t)	18	366.70	2178.86
1986	(1) (ϕ_t, p_t)	19	206.14	1465.05	(ϕ_t, p_t)	19	394.34	2077.61
	(2) (ϕ_t, p_c)	11	216.87	1459.00	(ϕ_t, p_c)	11	402.60	2069.29
	(3) (ϕ_{1-9}, p_c)	10	216.87	1456.94	(ϕ_{1-7}, p_c)	8	408.05	2068.60
1987	(1) (ϕ_t, p_t)	17	208.94	1507.28	(ϕ_t, p_t)	17	297.27	2014.57
	(2) (ϕ_t, p_c)	10	213.91	1497.68	(ϕ_t, p_c)	10	320.66	2023.50
	(3)				(ϕ_{1-7}, p_t)	16	297.57	2012.79
1988	(1) (ϕ_t, p_t)	15	174.13	1597.08	(ϕ_t, p_t)	15	149.74	1505.00
	(2) (ϕ_t, p_c)	9	176.65	1587.19	(ϕ_t, p_c)	9	181.50	1524.84
	(3)				(ϕ_{1-7}, p_t)	15	149.74	1505.48
1989	(1) (ϕ_t, p_t)	13	155.50	1209.73	(ϕ_t, p_t)	13	165.99	1426.97
	(2) (ϕ_t, p_c)	8	157.57	1201.39	(ϕ_t, p_c)	8	182.47	1431.05
1990	(1) (ϕ_t, p_t)	11	136.03	1135.37	(ϕ_t, p_t)	11	170.01	1423.97
	(2) (ϕ_t, p_c)	7	145.46	1136.53	(ϕ_t, p_c)	7	177.93	1423.67
1991	(1) (ϕ_t, p_t)	9	64.67	926.99	(ϕ_t, p_t)	9	58.02	1136.88
	(2) (ϕ_t, p_c)	6	68.63	924.76	(ϕ_t, p_c)	6	64.46	1137.16
1992	(1) (ϕ_t, p_t)	7	40.09	706.69	(ϕ_t, p_t)	7	47.27	862.72
	(2) (ϕ_t, p_c)	5	43.87	706.34	(ϕ_t, p_c)	5	48.89	860.23

- ϕ_t : Time-dependent survival rate.
 ϕ_c : Constant survival rate.
 p_t : Time-dependent capture probability.
 $\phi_{1-7/9}$: Survival probability constant after year six/eight.

Table 8. Survival of southern elephant seals born at Marion Island averaged over the cohorts 1983-1992 (survival adjusted for tag loss).

Age (x)	<u>MALES</u>			<u>FEMALES</u>		
	ϕ	S.E.(ϕ)	p	ϕ	S.E.(ϕ)	p
1	0.586	0.037	0.684	0.628	0.035	0.714
2	0.754	0.051	0.700	0.807	0.048	0.714
3	0.742	0.062	0.686	0.783	0.054	0.708
4	0.636	0.073	0.705	0.810	0.064	0.699
5	0.726	0.088	0.687	0.771	0.068	0.746
6	0.748	0.091	0.693	0.758	0.073	0.732
7	0.695	0.094	0.687	0.778	0.069	0.799
8	0.747	0.089	0.687	0.749	0.066	0.709
9	0.586	0.106	0.687	0.737	0.075	0.795
10	0.654	0.128	0.687	0.755	0.081	0.733
11	0.678	0.091	0.687	0.762	0.030	0.819
12	0.756	0.077	0.687	0.781	0.211	0.728
13	0.000	0.000	0.687	0.710	0.050	0.731

Table 9. Survival of southern elephant seals born at Marion Island in 1983 (survival adjusted for tag loss).

Age (x)	<u>MALES</u>			<u>FEMALES</u>		
	ϕ	S.E.(ϕ)	p	ϕ	S.E.(ϕ)	p
1	0.651	0.045	0.592	0.647	0.042	0.648
2	0.710	0.061	0.592	0.727	0.054	0.648
3	0.752	0.074	0.592	0.881	0.063	0.648
4	0.708	0.085	0.592	0.674	0.068	0.648
5	0.713	0.098	0.592	0.915	0.078	0.648
6	0.830	0.119	0.592	0.732	0.040	0.648
7	0.748	0.134	0.592	0.710	0.050	0.648
8	0.747	0.154	0.592	0.710	0.050	0.648
9	0.926	0.201	0.592	0.710	0.050	0.648
10	0.821	0.258	0.592	0.710	0.050	0.648
11	0.664	0.124	0.592	0.710	0.050	0.648
12	0.672	0.146	0.592	0.710	0.050	0.648
13	0.000	0.000	0.592	0.710	0.050	0.648

Table 10. Survival of southern elephant seals born at Marion Island in 1984 (survival adjusted for tag loss).

Age (x)	<u>MALES</u>			<u>FEMALES</u>		
	ϕ	S.E.(ϕ)	p	ϕ	S.E.(ϕ)	p
1	0.605	0.042	0.619	0.545	0.036	0.725
2	0.664	0.060	0.619	0.817	0.051	0.725
3	0.549	0.066	0.619	0.675	0.057	0.725
4	0.764	0.089	0.619	0.844	0.061	0.725
5	0.847	0.113	0.619	0.831	0.067	0.725
6	0.618	0.126	0.619	0.812	0.075	0.725
7	0.515	0.147	0.619	0.851	0.035	0.725
8	0.682	0.207	0.619	0.851	0.035	0.725
9	0.839	0.127	0.619	0.851	0.035	0.725
10	0.839	0.127	0.619	0.851	0.035	0.725
11	0.839	0.127	0.619	0.851	0.035	0.725
12	0.839	0.127	0.619	0.851	0.035	0.725

Table 11. Survival of southern elephant seals born at Marion Island in 1985 (survival adjusted for tag loss).

Age (x)	<u>MALES</u>			<u>FEMALES</u>		
	ϕ	S.E.(ϕ)	p	ϕ	S.E.(ϕ)	p
1	0.644	0.033	0.647	0.645	0.032	0.688
2	0.706	0.044	0.647	0.789	0.051	0.548
3	0.717	0.052	0.647	0.828	0.066	0.515
4	0.784	0.065	0.647	0.927	0.103	0.456
5	0.584	0.068	0.647	0.626	0.086	0.510
6	0.833	0.088	0.647	0.745	0.033	0.533
7	0.867	0.114	0.647	0.726	0.037	0.709
8	0.493	0.115	0.647	0.726	0.037	0.619
9	0.530	0.113	0.647	0.726	0.037	0.936
10	0.530	0.113	0.647	0.726	0.037	0.879
11	0.530	0.113	0.647	0.726	0.037	1.000

Table 12. Survival of southern elephant seals born at Marion Island in 1986 (survival adjusted for tag loss).

Age (x)	<u>MALES</u>			<u>FEMALES</u>		
	ϕ	S.E.(ϕ)	p	ϕ	S.E.(ϕ)	p
1	0.584	0.035	0.655	0.703	0.034	0.630
2	0.808	0.050	0.655	0.759	0.042	0.630
3	0.748	0.061	0.655	0.853	0.044	0.630
4	0.559	0.064	0.655	0.948	0.051	0.630
5	0.871	0.087	0.655	0.732	0.059	0.630
6	0.706	0.104	0.655	0.765	0.069	0.630
7	0.584	0.123	0.655	0.732	0.041	0.630
8	0.605	0.172	0.655	0.732	0.041	0.630
9	0.425	0.159	0.655	0.732	0.041	0.630
10	0.425	0.159	0.655	0.732	0.041	0.630

Table 13. Survival of southern elephant seals born at Marion Island in 1987 (survival adjusted for tag loss).

Age (x)	<u>MALES</u>			<u>FEMALES</u>		
	ϕ	S.E.(ϕ)	p	ϕ	S.E.(ϕ)	p
1	0.569	0.033	0.683	0.656	0.032	0.662
2	0.792	0.047	0.683	0.899	0.055	0.554
3	0.756	0.057	0.683	0.685	0.053	0.657
4	0.603	0.062	0.683	0.885	0.059	0.633
5	0.861	0.083	0.683	0.732	0.060	0.845
6	0.609	0.094	0.683	0.712	0.068	0.750
7	0.564	0.114	0.683	0.667	0.058	0.875
8	0.956	0.187	0.683	0.667	0.058	0.784
9	0.211	0.131	0.683	0.667	0.058	0.960

Table 14. Survival of southern elephant seals born at Marion Island in 1988 (survival adjusted for tag loss).

Age (x)	<u>MALES</u>			<u>FEMALES</u>		
	ϕ	S.E.(ϕ)	p	ϕ	S.E.(ϕ)	p
1	0.618	0.033	0.690	0.603	0.036	0.689
2	0.757	0.045	0.690	0.727	0.050	0.681
3	0.745	0.053	0.690	0.800	0.054	0.683
4	0.692	0.064	0.690	0.857	0.060	0.778
5	0.649	0.075	0.690	0.652	0.061	0.880
6	0.746	0.094	0.690	0.774	0.041	0.919
7	0.671	0.108	0.690	0.893	0.054	1.000
8	1.000	0.166	0.690	0.805	0.060	0.805

Table 15. Survival of southern elephant seals born at Marion Island in 1989 (survival adjusted for tag loss).

Age (x)	<u>MALES</u>			<u>FEMALES</u>		
	ϕ	S.E.(ϕ)	p	ϕ	S.E.(ϕ)	p
1	0.550	0.036	0.635	0.616	0.036	0.640
2	0.898	0.051	0.635	0.884	0.061	0.563
3	0.865	0.069	0.635	0.716	0.061	0.778
4	0.432	0.062	0.635	0.651	0.062	0.761
5	0.629	0.096	0.635	0.732	0.075	0.828
6	0.888	0.125	0.635	0.626	0.084	0.818
7	0.917	0.181	0.635	0.867	0.087	0.849

Table 16. Survival of southern elephant seals born at Marion Island in 1990 (survival adjusted for tag loss).

Age (x)	<u>MALES</u>			<u>FEMALES</u>		
	ϕ	S.E.(ϕ)	p	ϕ	S.E.(ϕ)	p
1	0.607	0.040	0.657	0.664	0.033	0.732
2	0.701	0.053	0.814	0.813	0.041	0.732
3	0.741	0.063	0.679	0.754	0.048	0.732
4	0.730	0.073	0.867	0.777	0.053	0.732
5	0.628	0.097	0.684	0.841	0.061	0.732
6	0.754	0.083	0.736	0.895	0.089	0.732

Table 17. Survival of southern elephant seals born at Marion Island in 1991 (survival adjusted for tag loss).

Age (x)	<u>MALES</u>			<u>FEMALES</u>		
	ϕ	S.E.(ϕ)	p	ϕ	S.E.(ϕ)	p
1	0.601	0.035	0.848	0.642	0.034	0.771
2	0.730	0.044	0.848	0.808	0.042	0.790
3	0.775	0.053	0.848	0.824	0.045	0.838
4	0.543	0.064	0.848	0.724	0.050	0.912
5	0.752	0.094	0.848	0.876	0.042	0.868

Table 18. Survival of southern elephant seals born at Marion Island in 1992 (survival adjusted for tag loss).

Age (x)	<u>MALES</u>			<u>FEMALES</u>		
	ϕ	S.E.(ϕ)	p	ϕ	S.E.(ϕ)	p
1	0.430	0.035	0.808	0.558	0.035	0.821
2	0.777	0.053	0.808	0.844	0.040	0.821
3	0.769	0.066	0.808	0.811	0.048	0.821
4	0.545	0.086	0.808	0.809	0.068	0.821

Table 19.Life table for male southern elephant seals from Marion Island (survival estimates averaged over cohorts 1983-1992).

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.414	0.414	0.586
1	0.586	0.144	0.246	0.754
2	0.442	0.114	0.258	0.742
3	0.328	0.119	0.364	0.636
4	0.209	0.057	0.274	0.726
5	0.151	0.038	0.252	0.748
6	0.113	0.035	0.305	0.695
7	0.079	0.020	0.253	0.747
8	0.059	0.024	0.414	0.586
9	0.034	0.012	0.346	0.654
10	0.023	0.007	0.322	0.678
11	0.015	0.004	0.244	0.756
12	0.012	0.012	1.000	0.000
13	0.000			

Table 20.Life table for female southern elephant seals from Marion Island (survival estimates averaged over the cohorts 1983-1992).

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.372	0.372	0.628
1	0.628	0.121	0.193	0.807
2	0.507	0.110	0.217	0.783
3	0.397	0.075	0.190	0.810
4	0.321	0.074	0.229	0.771
5	0.248	0.060	0.242	0.758
6	0.188	0.042	0.222	0.778
7	0.146	0.037	0.251	0.749
8	0.109	0.029	0.263	0.737
9	0.081	0.020	0.245	0.755
10	0.061	0.014	0.238	0.762
11	0.046	0.010	0.219	0.781
12	0.036	0.011	0.290	0.710
13	0.026			

Table 21. Comparison of mean age-specific survival estimates for the elephant seal population at Marion Island over two discrete time periods.

Age	Cohorts	<u>MALES</u>		<u>FEMALES</u>	
		Survival	Difference	Survival	Difference
0	1983-1987	0.611		0.639	
	1988-1992	0.561	-5.0%	0.616	-2.3%
1	1983-1987	0.736		0.798	
	1988-1992	0.773	+3.7%	0.815	+1.7%
2	1983-1987	0.704		0.784	
	1988-1992	0.779	+7.5%	0.781	-0.3%
3	1983-1987	0.684		0.856	
	1988-1992	0.588	-9.6%	0.764	-9.2%
4	1983-1987	0.775		0.767	
	1987-1991	0.703	-7.2%	0.767	0%
5	1983-1986	0.747		0.764	
	1987-1990	0.749	+0.2%	0.752	-1.2%
6	1983-1986	0.679		0.755	
	1986-1989	0.684	+0.5%	0.790	+3.5%

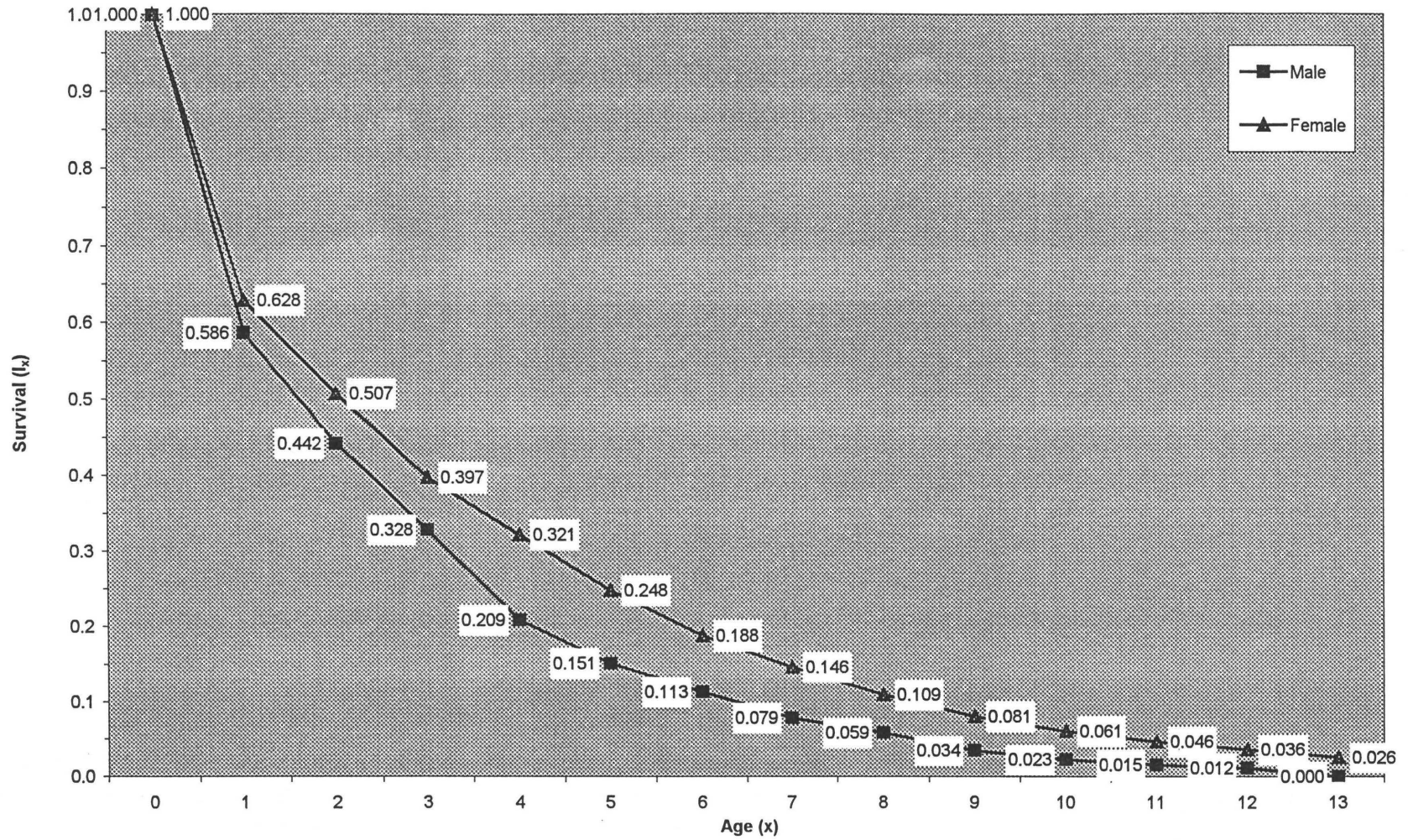


Figure 5. Survival of southern elephant seals at Marion Island (survivorship averaged over the period 1983–1992).

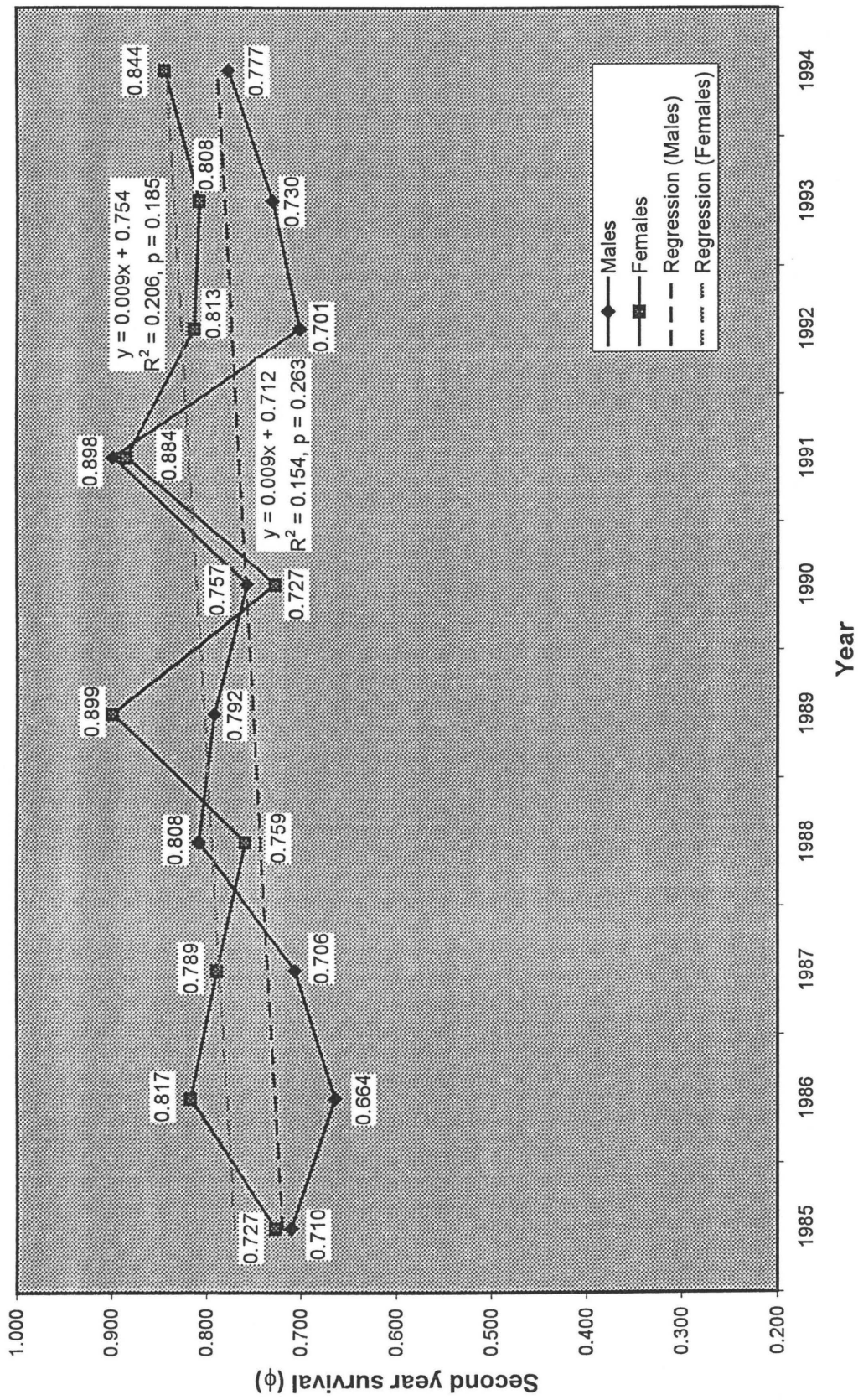


Figure 7. Inter-cohort comparison (1983-1992) of second year survival for southern elephant seals from Marion Island.

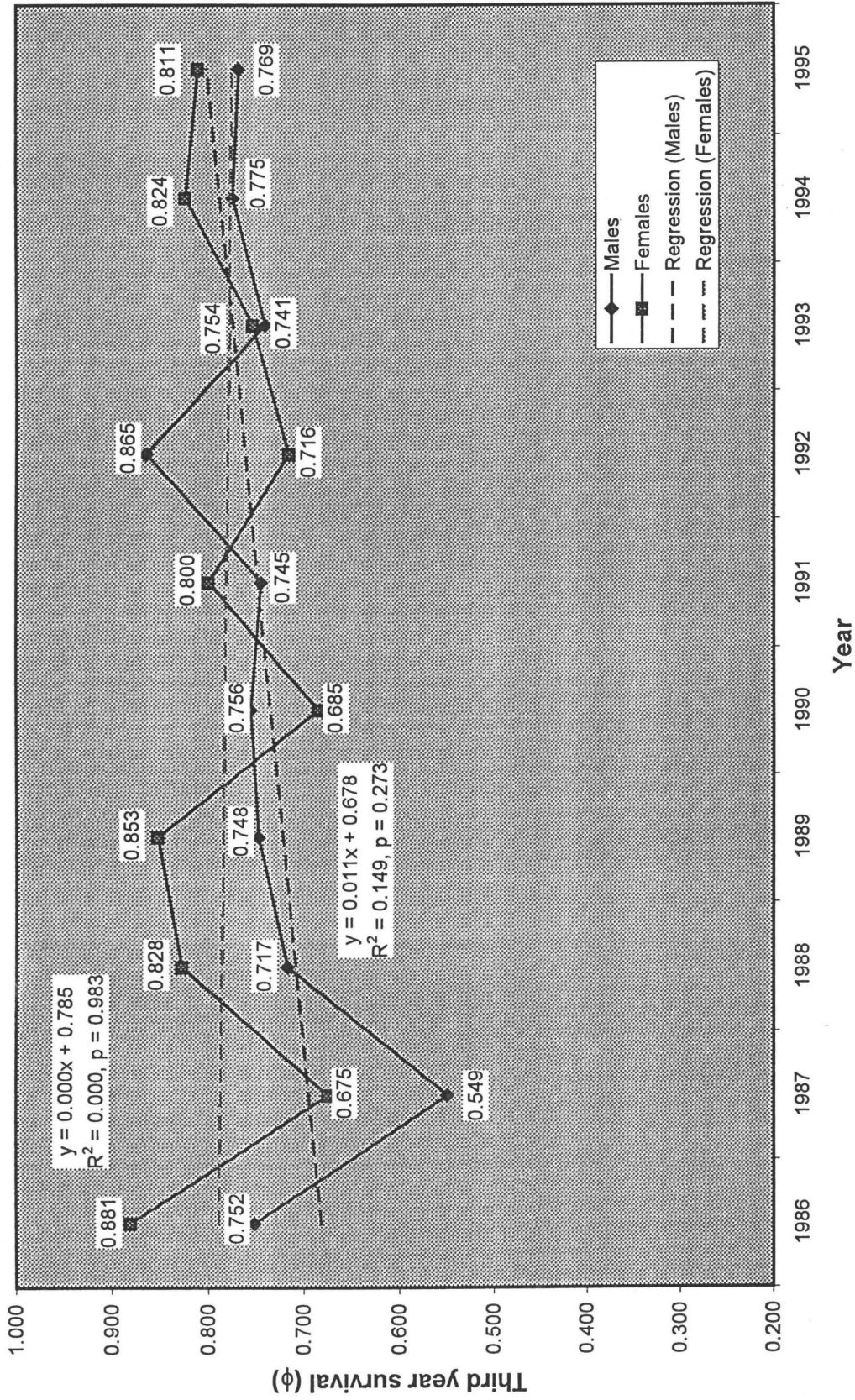


Figure 8. Inter-cohort comparison (1983-1992) of third year survival for southern elephant seals from Marion Island.

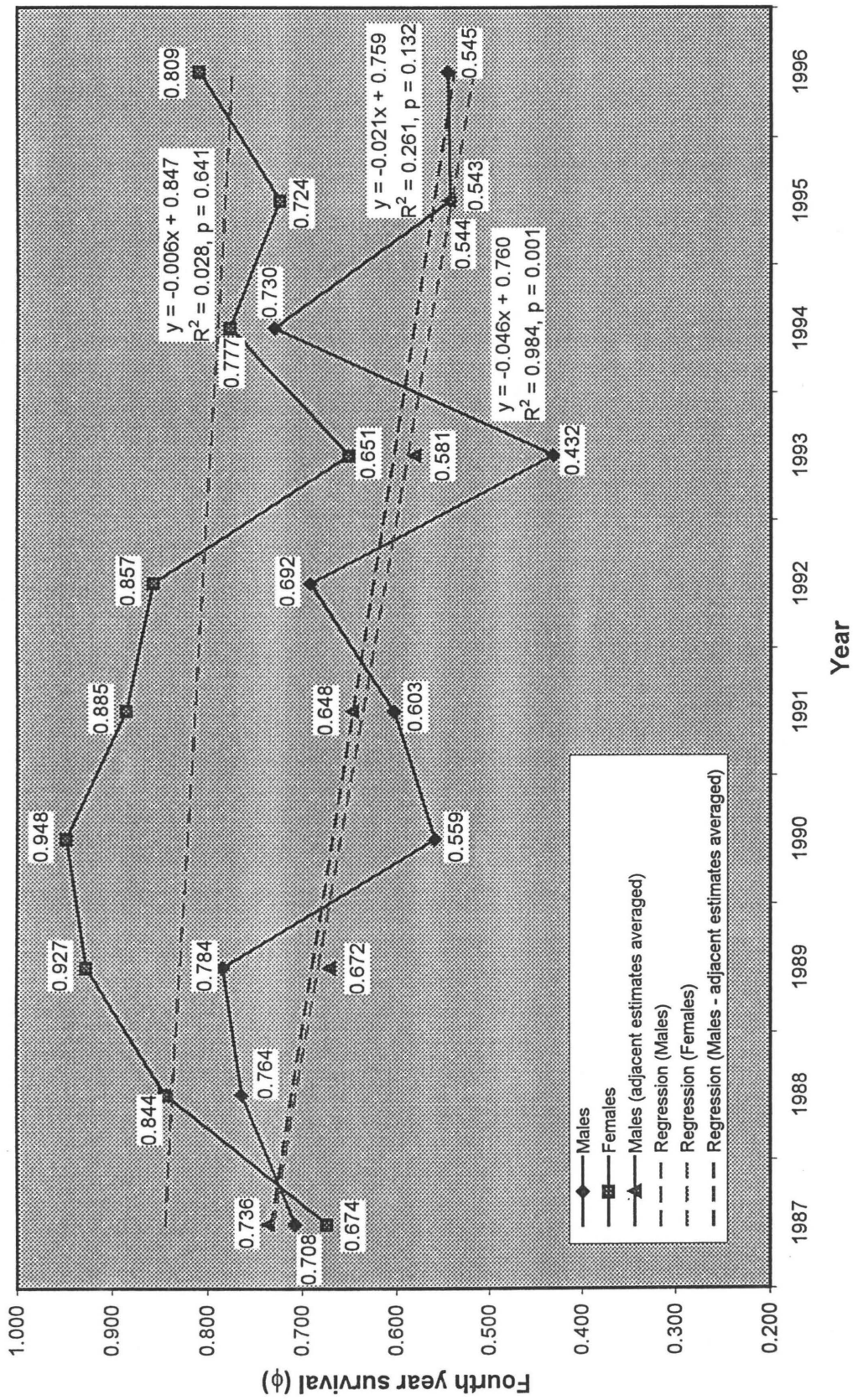


Figure 9. Inter-cohort comparison (1983-1992) of fourth year survival for southern elephant seals from Marion Island.

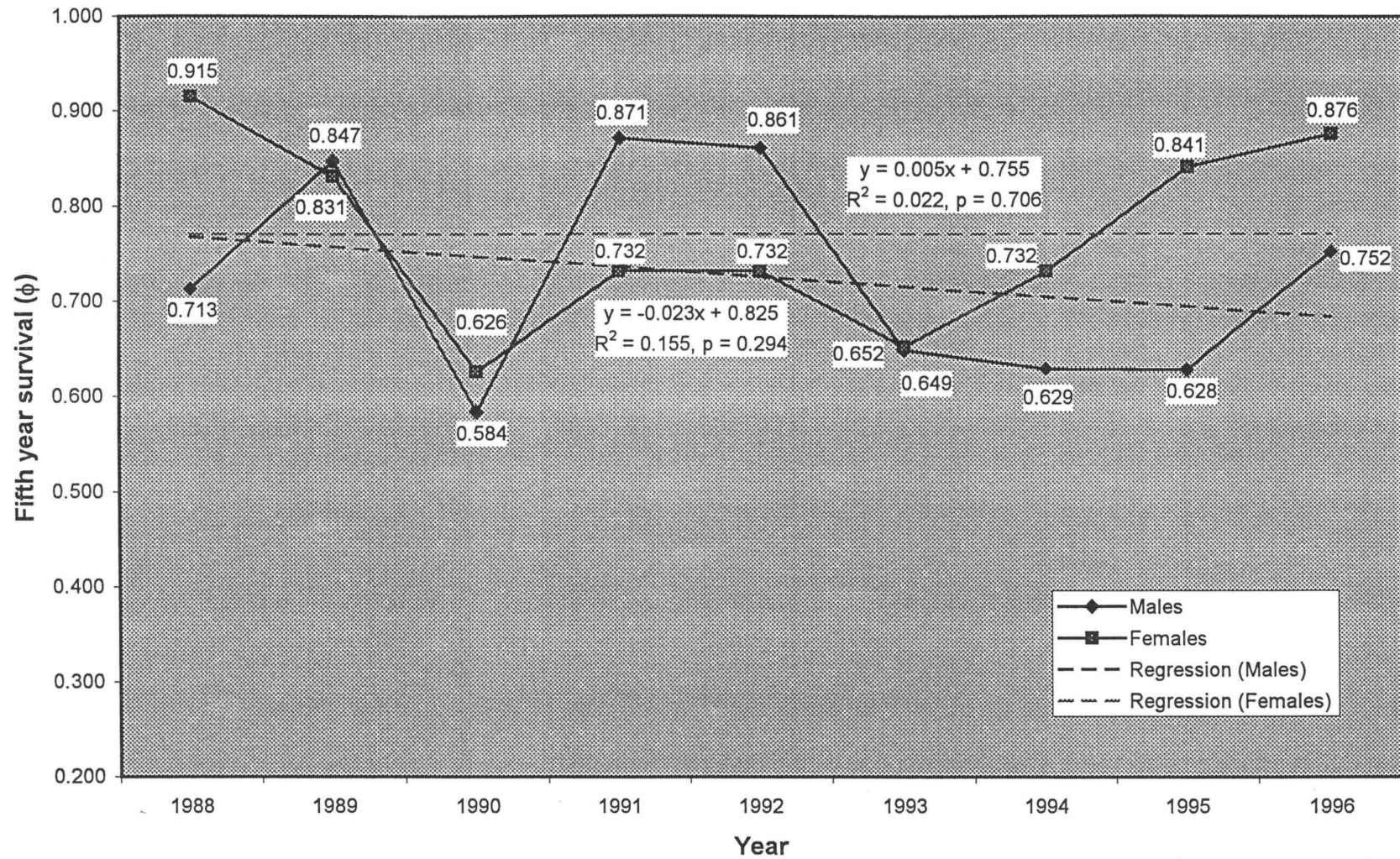


Figure 10. Inter-cohort comparison (1983-1991) of fifth year survival for southern elephant seals from Marion Island.

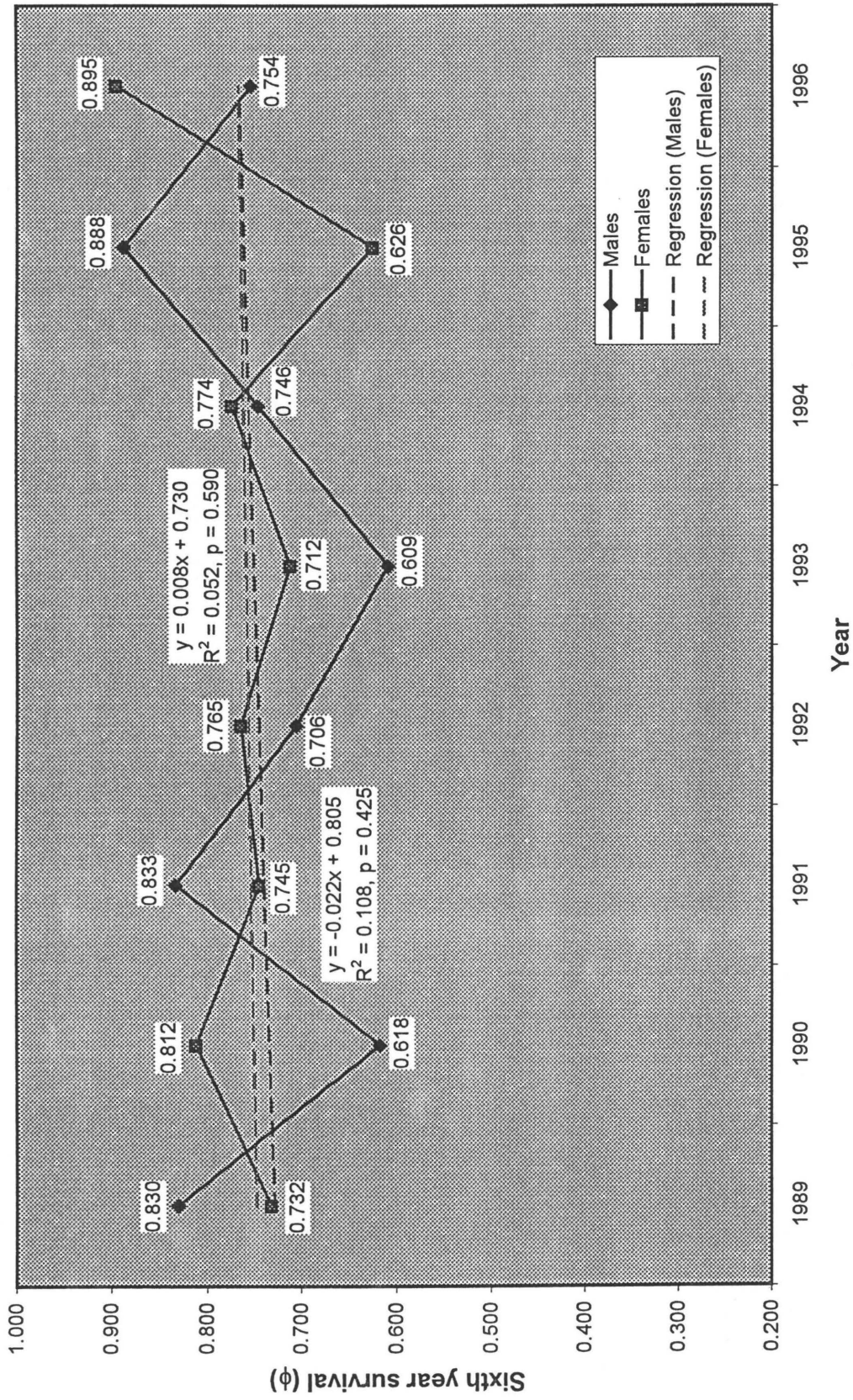


Figure 11. Inter-cohort comparison (1983-1990) of sixth year survival for southern elephant seals from Marion Island.

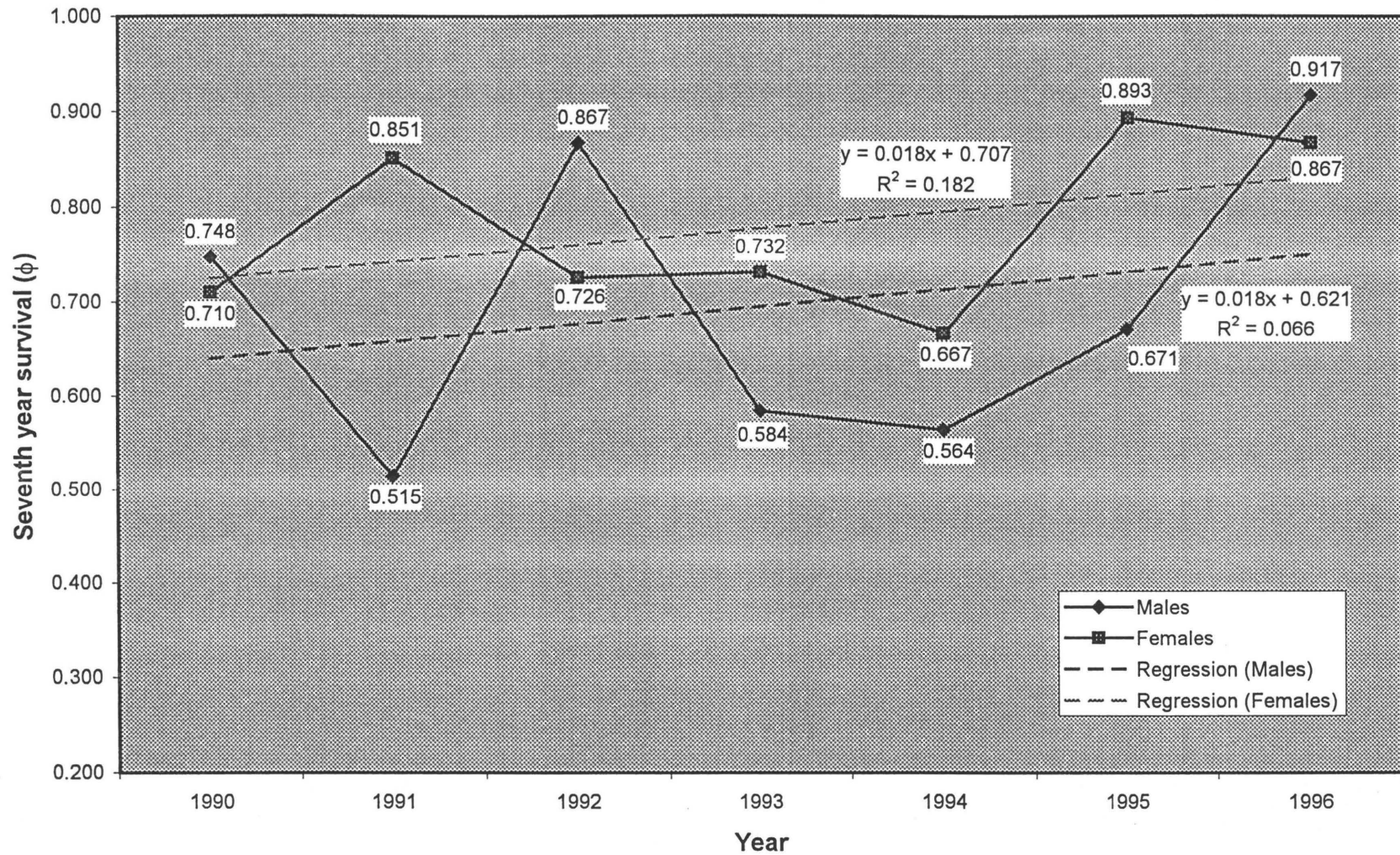


Figure 12. Inter-cohort comparison (1983-1989) of seventh year survival for southern elephant seals from Marion Island.

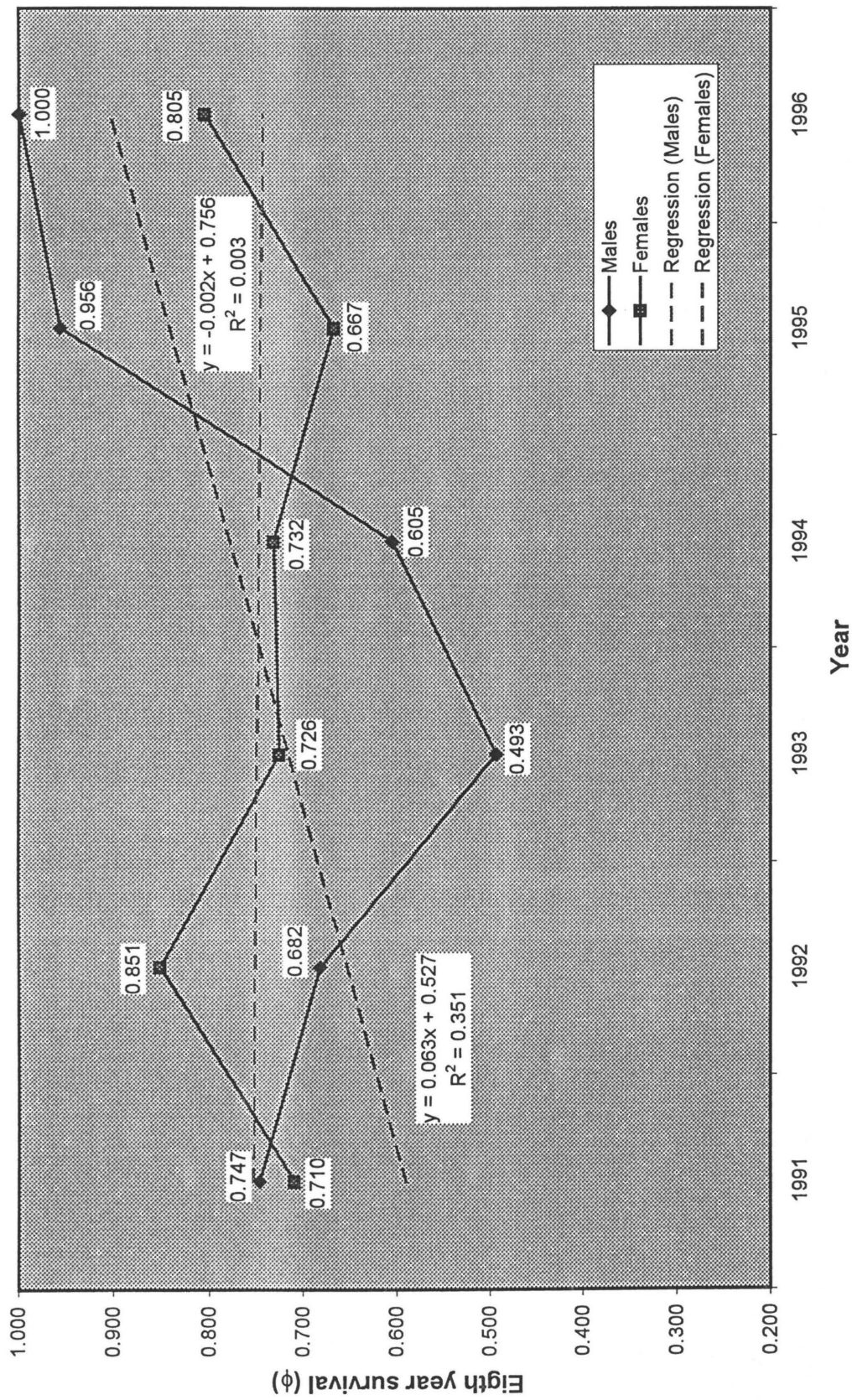


Figure 13. Inter-cohort comparison (1983-1988) of eighth year survival for southern elephant seals on Marion Island.

corresponds to a high second and third year male mortality (Figs 7 and 8) in 1987. A high female mortality in the fourth year for the 1989 cohort similarly corresponds to a high female mortality in the fifth year for the 1988 cohort (Figs 9 and 10), hence a high mortality in 1993. This is supported by the high first year mortality (Fig. 6), third year male mortality (Fig. 8), fourth year male mortality (Fig. 9), fifth year male mortality (Fig. 10), and sixth and seventh year male mortality (Figs 11 and 12) in 1993. Although not as clear, a similar picture holds for 1990. Females of the 1987 cohort in their third year and females of the 1985 cohort in their fifth year experienced high mortalities, although females in their fourth year in the 1986 cohort experienced extremely low mortality. In addition, in 1990 high mortalities were also experienced by first year males (Fig. 6), second year females (Fig. 7), third year females (Fig. 8), fourth year males (Fig. 9), fifth year males and females (Fig. 10), and sixth year males (Fig. 11). The elephant seal population on Marion Island therefore experienced exceptionally high rates of mortality in 1987, 1990, and 1993.

Variation in age-specific survival rates among cohorts was substantially lower up to age three than for older animals (mean coefficient of variation (CV) is 9.1% compared to 14.6% for ages three to six; CV estimates for older animals are not taken into account due to a likely increase as a function of smaller sample sizes).

4.4 Discussion

A decline in numbers of a population that is not subject to immigration or emigration is caused by a decrease in survival and/or reproductive success (York 1994). The known

dispersion and dispersal of elephant seals from Marion Island have been summarized (Bester 1989; Jonker & Bester 1998; Malherbe 1998), with the only noteworthy emigration being to Ile de la Possession, where they are mostly observed during the moulting phase. A single three-year-old female from Marion Island gave birth on Possession Island in 1988, and a five-year-old female with a pup was sighted on Hog Island in 1989 (Guinet *et al.* 1992). Movement of elephant seals (mostly juveniles), have been recorded between Marion Island and Prince Edward Island, 23 km to the northeast (Panagis 1981; Bester 1989). Nevertheless, emigration appears to be limited and is assumed to have a negligible effect upon the dynamics of the Marion Island elephant seal population.

Fecundity is well recognized as an important parameter relating to the dynamics of a population (Caughley 1977; Krebs 1985). Population growth rate in large mammals is, however, more influenced by survival than by fecundity (Choquenot 1991; Lima & Paez 1997; Saether 1997). Bester & Wilkinson (1994) manipulated life table data from the Marion Island elephant seal population, and demonstrated that even when fecundity was set at a maximum, the population growth rate was still negative. Furthermore, the mean age at first pupping (1983 cohort) was similar to the stable South Georgia population (McCann 1985; Bester & Wilkinson 1994), and the apparent 100% pupping rates of females age six and older, were higher than the 85% and 97.8% recorded for southern and northern elephant seals respectively (McCann 1985; Le Boeuf & Reiter 1988; Bester & Wilkinson 1994). The population decline must therefore be a consequence of either a decrease in adult survival, juvenile survival or a combination of these.

4.4.1 Age-specific survival

A previous long term study on life-history parameters of southern elephant seals at Macquarie Island, was reported by Hindell (1991). While the accuracy of the study was reduced by the acknowledged violation of several assumptions, including that of consistency of search effort, it is still useful for comparison. Another recognised weakness in that study, which was based on the number of animals known to be alive in each age-class for each cohort, is that juvenile survival may have been underestimated due to lower levels of philopatry, relative to adults. This may explain, to some extent, the low first year survival estimates found during that study (0.459 and 0.425 for males and females respectively in the 1950's; 0.292 and 0.241 in the 1960's). More recently the renewed mark-recapture program at Macquarie Island revealed first year survival estimates (65.6%: McMahon *et al.* 1999) falling within the range recorded in the present study (Fig. 6). With the exception of nine- and 12-year-old males and three-, eight- and 11-year-old females, Hindell's (1991) estimated survival rates for all post year one age categories of Macquarie Island elephant seals were higher than those recorded for the Marion Island population (present study). Males aged three up to seven exhibited survival rates in excess of 6% higher than those found for equivalent age categories at Marion Island. Considering that these are minimum estimates (calculated from 'known to be alive' animals), it seems likely that adult survival is substantially higher at Macquarie Island than at Marion Island.

The survival rates found in the present study are representative of a declining population. Comparison with a stable population could highlight parameters that are incisive in the decline. Survival data for the stable South Georgia elephant seal population

is available in the form of stationary life tables that are based on age-structure data (McCann 1985). Although this method of obtaining survival data has in recent years been increasingly criticized because of the assumptions that are made (e.g., stability of age structure, random sampling, and stationary population size over time) (Loison *et al.* 1994; Gaillard *et al.* 1993), it is often the only practical means of obtaining survival estimates for a population. By utilising the standing age distribution for the Marion Island elephant seal population over the period 1989-1991 (chapter 6), it was possible to obtain survival data comparable to that for the South Georgia population (by dividing the number of individuals in each age category by those in the preceding age category = p_x and averaging it over the four age distributions). Juvenile mortality rate, equated over the first three years of life, was slightly higher for the South Georgia population (24.1% and 22.3% compared to 22.7% and 20.5%, for males and females respectively). This militates against the likelihood that juvenile mortality is the driving force behind the Marion Island elephant seal population decline. When considering survival from ages three to eight, the converse is true (19.2% versus 30.1% annual mortality for males, and 12% versus 21.7% annual mortality for females). The comparison emphasizes that adult mortality, rather than juvenile mortality, is an important parameter in the population decline of elephant seals at Marion Island.

Other studies that reported on survival, in which large mammals were followed through time, include Boyd *et al.* (1995), who calculated an average survival rate of 0.83 for female Antarctic fur seals, and Croxall & Hiby (1983) and Testa & Siniff (1987) who reported survival rates of 0.80 and 0.85 respectively for adult female Weddell seals. Toigo *et al.* (1997) found an average adult survival of 0.97 for Alpine ibex (*Capra ibex ibex*), and

Loison *et al.* (1994) described juvenile and adult survival rates of 0.58 and 0.96 respectively for female chamois (*Rupicapra rupicapra*). These results further emphasize the relatively high juvenile and low adult survival of elephant seals on Marion Island.

The elephant seals on Marion Island were only tagged once they were successfully weaned. Pre-weaning mortality was therefore not included in the mark-recapture estimates, similar to other first year survival estimates based on the resightings of marked elephant seals (Le Boeuf *et al.* 1994). Pre-weaning mortality at Marion Island (4.0%; 1983-1997, Appendix I) is lower than that for the stable South Georgia population (4.5%; McCann 1985) suggesting that mortality at this stage is negligible in terms of the population decline at Marion Island.

Several studies have addressed one of the fundamental problems in population biology, namely what impact the different vital rates have on the overall variability in population growth rate. Eberhardt (1981) suggested that juvenile survival is a key component of population dynamics and a potential indicator of population status in large mammal populations. Increases in population size have been shown to occur among four different pinniped species when juvenile survival was high, while prolonged periods of low juvenile survival were documented during periods of population declines, for the same species (Eberhardt & Siniff 1977). This contrasts with the results presented in this chapter. The elephant seal population at Marion Island has been declining steadily despite its relatively high juvenile survival rate. Adult survival has also been considered to be one of the most important demographic parameters of large mammal populations, and their growth rates have been recorded as being consistently more sensitive to adult survival than

to any other vital rate (Eberhardt 1985; Walsh *et al.* 1995; Toigo *et al.* 1997). Adult female survival is considered particularly influential in relation to population growth (Eberhardt 1985; Taylor *et al.* 1987; Walsh *et al.* 1995). Although adult female survival is substantially higher than that of adult males in the present study, it is still considerably lower than the survival estimates of adult females in the studies mentioned above. It would appear that changes in the Marion Island population have been affected by adult, in particular adult female, rather than by juvenile survival. Adult survival could conceivably be affected by the availability of food which has been discussed as one of the possible reasons for the decline of elephant seal populations (see Hindell 1991; Hindell *et al.* 1994). The relatively high juvenile survival found in this study argues against predation by killer whales (*Orcinus orca*) as an important factor relating to the population decline at Marion Island (see Condy *et al.* 1978; Guinet *et al.* 1992).

4.4.2 Sex-related survival

The principal disparity in adult survival in many species is often sex-related (Toigo *et al.* 1997). In many mammals, males suffer greater mortality rates than females (Roff & Bowen 1983). This is especially true for sexually dimorphic, polygynous mammals, among which male mortality is likely to increase with the attainment of sexual maturity (McCann 1985). The differences in survival between sexes of various mammals appear positively correlated to their degree of sexual dimorphism (Promislow 1992). Reasons for this disparity in survival have been attributed to male-male competition and greater susceptibility of large-bodied males to nutritional stress (Clutton-Brock *et al.* Cited in

Toigo *et al.* 1997). Considering that southern elephant seals are the most sexually dimorphic mammals, and that sexual dimorphism becomes pronounced after 12 months of age (Bell *et al.* 1997), it is not surprising that males of this species have higher mortality rates than females.

Siniff *et al.* (1977) suggested that wounds received and energy expended in the defence of underwater territories, could lead to the higher mortality observed for male Weddell seals. While no evidence exists to suggest that wounds received by male-male interactions result in the mortality of elephant seal males from Marion Island, increased energy expenditure during the breeding season may be a contributing factor. In addition, the greater year round absolute energy requirements of males may cause them to be more prone to starvation during periods of food shortage. Survival costs incurred by the sexually dimorphic Alpine ibex male in the maintenance of their large-bodied phenotype, have been shown to be negligible in the absence of resource limitation (Toigo *et al.* 1997). This supports the notion that the increased food requirements among males of sexually dimorphic species cause a discrepancy in survival between the sexes, and could explain the sexual differences in survival of southern elephant seals from Marion Island. This argument, however, does not hold for the stable South Georgia population, where the sex ratio showed an even stronger bias towards the female component (McCann 1985; chapter six).

4.4.3 Inter-cohort survival

Although the pattern of variation in survival rates constitutes an important determinant of vertebrate population dynamics (Gaillard *et al.* 1993), the degree to which survival among mammals varies between years remains largely unknown (Jorgenson *et al.* 1997). Jorgenson *et al.* (1997) showed that yearling survival among bighorn sheep is more sensitive to between year environmental fluctuations than adult survival. A similar pattern was observed for populations of 14 other species of large herbivore (Gaillard *et al.* 1998). It has been argued that juveniles are more susceptible to stress induced by environmental fluctuation due to immature immune systems, small size, inexperience, or a combination of these, and thus have more variable mortality rates than adults (Promislow & Harvey 1990). While there is much evidence indicating that juveniles of large mammal species have more variable survival rates than adults, the opposite is the case among Marion Island elephant seals. Although substantial year to year variation in survival in the first year was apparent, it was much lower than in subsequent age-classes. This seems to indicate a relative insensitivity of first year survival to any environmental fluctuations that occurred during the study period. Juvenile survival is highly sensitive to limiting factors (Gaillard *et al.* 1998), and with the relatively high and constant survival of seals in their first year at Marion Island, it would appear that they are not constrained by any lack of resources within their, as yet undetermined (Bester 1989), foraging range. This furthermore provides possible indication of separate foraging grounds, or foraging strategies, between first year and adult elephant seals, although Slip (1997) presented some evidence to the contrary.

The natural rates of population increase of large mammal species are influenced more by changes in survival than in fecundity (Bester & Wilkinson 1994; Lima & Paez 1997; Saether 1997), and are often more sensitive to prime-age adult than juvenile survival (Eberhardt 1985; Escos *et al.* 1994). In most marine mammals only a small change in adult survival is required to alter population growth (Eberhardt & Siniff 1977). It has been demonstrated that a mere 5% increase in adult survival could stabilize two rapidly declining populations of Spanish ibex (*Capra pyrenaica*), whereas a 5% decrease could destabilize a stable population (Escos *et al.* 1994). Bearing in mind: (1) the importance of adult survival in determining population change, (2) the relatively high, and stable nature of Marion Island juvenile survival, and (3) the comparatively low and still decreasing adult survival rates of southern elephant seals on Marion Island, it would seem that the proximate factor responsible for the elephant seal decline at Marion Island is the decrease in adult survival.

Bester & Wilkinson (1994) showed that there was an increase in mortality of three-year-old females in the 1983 cohort on Marion Island. A re-analysis of the cohort, with additional recapture data, illustrated the same increase, although it was not evident when averaging the survival values from all the cohorts. The average mortality of three-year-old females have, however, increased significantly over the study period (Table 21). This is significant since at this stage a number of three-year-olds have been recruited to the breeding population (see section 5.3). The remaining three-year-olds are therefore on the verge of entering the adult population, and an increase in mortality at this stage would negatively impact upon the population. This is also a time when females are exposed to increased physiological stress and energetic demands imposed by gestation and the

postpartum lactation period (Bester & Wilkinson 1994), which would be exacerbated by the phase of continuing body growth which would also increase energetic demands relative to the older females (Laws 1953; Laws 1956 (c); Reiter *et al.* 1981; Reiter & Le Boeuf 1991). Furthermore, a decrease in fourth and fifth year survival of elephant seal males occurred over the study period (Table 21). During this stage, southern elephant seal males undergo a spurt of secondary growth (Ling & Bryden 1981; Laws 1984), and food requirements are greatly increased. It is therefore suggested that the decline in survival of males in their fourth and fifth year of life, and females in their fourth year, strongly points to food limitation as the ultimate cause behind the overall population decline at Marion Island.

CHAPTER 5 REPRODUCTIVE PARAMETERS

5.1 Introduction

The dynamics of a population are governed by the balance between birth rates and death rates. The factors which influence these rates may be attributed to extrinsic effects, such as density-dependent mortality, and intrinsic effects, such as senescence or changing fecundity with age (Boyd *et al.* 1994; Hindell 1991). The fecundity or recruitment schedule, together with the survival schedule and the age distribution, are the three factors that determine population growth rate in discrete age-structured populations (Taylor *et al.* 1987). Despite the certitude that fecundity has often been considered as playing a secondary role to age-specific survival in the growth of a population (Bester & Wilkinson 1994; Lima & Paez 1997), it is still integral to population maintenance. It appears that the onset of sexual maturity in females of large mammal species is the demographic variable that first responds to resource limitation (Fowler 1987; Owen-Smith 1990), and reproductive rates can therefore also be useful in terms of providing an index to environmental changes.

Recently weaned southern elephant seals have been tagged on an annual basis at Marion Island since 1983 (chapter three) as part of a long term study on the dynamics of the population (Bester 1988). Chapter four described the survival of the population relative to age, sex and time. As animal populations often exhibit changes in reproductive parameters following marked changes in population size (Bowen *et al.* 1981), this chapter focuses on age-specific fecundity and the changes in these rates over time, as well as age of sexual maturity in the population. Such changes in breeding performance over time is by and large a function of extrinsic factors that relate to spatial or temporal differences such as food availability and weather (Lunn *et al.* 1994). Despite the importance of reproductive parameters in population biology, very few long term studies have been performed. Amongst the few are studies by Siniff *et al.* (1977) and Testa & Siniff (1987) on Weddell seals (*Leptonychotes weddellii*), Le Boeuf & Reiter (1988) and Huber *et al.* (1991) on northern elephant seals (*Mirounga angustirostris*), Hindell (1991) on southern elephant seals and Lunn *et al.* (1994) on Antarctic fur seals (*Arctocephalus gazella*).

The fecundity rate of a female is measured as the number of live births she produces over an interval of time, and when used in analysis, it is expressed as the mean number of female live births per female over an interval of age (Caughley 1977). To determine age-specific fecundity rates the mean litter size, sex ratio at birth, and mean number of litters produced per year need to be identified for each age class (Caughley 1977). An elephant seal female usually only produces a single pup (King 1983; Laws 1994), which leaves the sex ratio at birth and pupping frequency to be determined. The analysis in this chapter is therefore primarily focused on determining the mean number of litters produced per year and the sex ratio at birth in ten cohorts (1983-1992) of elephant

seals. Since the former never exceeds one in elephant seals, it translates into estimating the proportion of females that give birth in a specified year.

5.2 Methods

From 1983 to 1996, a total of 6924 recently weaned elephant seal pups were tagged and sexed at Marion Island (see section 3.2), allowing assessment of the sex ratio at birth.

An extensive recapture program commenced in 1983 (chapter four), and during the breeding seasons (mid-August to mid-November) all the beaches occupied by elephant seals were searched on a weekly basis for tagged individuals. Multiple sightings in a breeding season were treated as a single sighting. Capture history matrices were constructed using this recapture data for the cohorts 1983-1992. These were subsequently used as input files to be analyzed by the computer package MARK (G White, University of Colorado), designed to obtain maximum likelihood estimates of survival and capture probability rates from the resighting of marked individuals. Where in accordance with the Akaike Information Criterion (AIC), survival parameters were maintained constant so as to increase the accuracy of the capture probability estimates (see Anderson *et al.* 1994).

The capture probabilities consisted of two components. The first represents the probability that a seal in a given age category has hauled out during the breeding season. It is this component that is of interest, as it can be translated into the age-specific probability of an animal breeding. This is under the assumption that all females that haul out during the breeding season do so to give birth, as first time matings take place at sea (see Laws

1956b). The second component, which confounds breeding probability, represents the probability of not observing a female that hauled out during the breeding season. In order to estimate the first component, the second had to be assessed in order to account for females that were present but not observed.

Capture probabilities of females six years and older were used in order to derive the second component, i.e. the probability of not having observed females that were present on the beaches. Elephant seal females older than five years of age give birth virtually every year, and hence haul out with few exceptions (see Huber 1987) on an annual basis during the breeding season (Reiter *et al.* 1981; Le Boeuf & Reiter 1988; Wilkinson 1991). Females that are primiparous at an early age have been recorded to skip pupping the following year (Huber 1987), but after age five a similar reproductive pattern to females that delay onset of reproduction is expected (Wilkinson 1991). The probability of not sighting an individual that was present during the breeding season could therefore be determined by subtracting the capture probability of females older than five years of age from one. The capture probabilities of females older than five years of age were maintained constant, yielding a single capture probability for animals in each of the cohorts that had more than six years of capture history (1983-1990). Reproductive rates for most populations of large mammals quickly “plateau” at maturity (Caughley 1977). By maintaining adult, age-specific estimates as constant, a meaningful average value could therefore be calculated. The average value for the seven cohorts were subtracted from one, and this value was added onto all the age-specific capture probability estimates in order for it to be representative of the age-specific breeding probabilities. It was assumed that a

constant proportion of females were positively identified during the various breeding seasons.

The age-specific fecundity rates were compared over the different cohorts to search for possible trends in both age at maturity and age-specific fecundity using Pearson's linear regression test.

5.3 Results

Of the tagged pups, 3475 individuals were positively identified as males and 3449 as females, yielding an effective sex-ratio of 1:1 (chapter three), assuming that it applies to newborns as well.

The number of parameters in the full time-dependent CJS model were reduced by eliminating nonsignificant effects, which is very important for obtaining precise estimates of resighting probabilities. The age-specific survival rate appeared unaffected by time/age (Table 22). Removing the effect of age on survival rate greatly reduced the number of parameters to be estimated. Maintaining the capture probabilities of females older than five years of age as constant, resulted in an enhanced parsimonious model (Table 22).

Resighting probabilities with standard errors obtained using the software program MARK are presented in Table 23. Using these values, breeding probabilities and fecundity rates were derived for the various age-categories belonging to the respective cohorts (Table 23).

Females gave birth for the first time at ages three to six. Among the cohorts 1983 to 1992, age-specific fecundity ranged from 0.152 to 0.346 in three-year-olds, from 0.262 to 0.5 in four-year-olds, and from 0.341 to 0.5 in five-year-olds. The probability of breeding increased with age up to six years of age, reflecting the progressive increase in the number of females attaining breeding status in the population. On average fecundity was 0.25 for three-year-olds, 0.42 for four-year-olds, and 0.44 for five-year-olds. A significant increase in fecundity rate over the study period was evident for three-, four- and five-year-old females (slope= 0.02 ± 0.004 ; $r^2=0.746$; $p=0.0013$; slope= 0.024 ± 0.006 ; $r^2=0.652$; $p=0.0047$; slope= 0.022 ± 0.005 ; $r^2=0.755$; $p=0.0024$ respectively) (Fig. 14). No trend in capture probability was observed for females six years of age and older (slope= 0.0148 ; $r^2=0.1241$; $p=0.392$). A general decrease in the age of maturity concordant with the population decline is clearly manifested.

Table 23. Age-specific fecundity rates acquired from capture probability estimates of breeding females in ten cohorts (1983-1992) of southern elephant seals at Marion Island.

Age	Cohort	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	Mean
0	Sample size	198	234	343	278	312	285	267	249	245	224	234
1	Capture probability	0	0	0	0	0	0	0	0	0	0	0
2	Capture probability	0	0	0	0	0	0	0	0	0	0	0
3	Capture probability	0.157	0.044	0.084	0.216	0.139	0.188	0.354	0.431	0.314	0.431	0.236
	Standard error	0.045	0.022	0.025	0.040	0.032	0.040	0.058	0.054	0.051	0.069	0.044
	Breeding probability	0.417	0.304	0.344	0.476	0.399	0.448	0.614	0.691	0.574	0.691	0.496
	Fecundity	0.209	0.152	0.172	0.238	0.200	0.224	0.307	0.346	0.287	0.346	0.248
4	Capture probability	0.370	0.264	0.329	0.705	0.592	0.735	0.588	0.653	0.830	0.794	0.586
	Standard error	0.076	0.059	0.053	0.056	0.057	0.061	0.077	0.060	0.054	0.133	0.069
	Breeding probability	0.630	0.524	0.589	0.965	0.852	0.995	0.848	0.913	1.000	1.000	0.832
	Fecundity	0.315	0.262	0.295	0.483	0.426	0.498	0.424	0.457	0.500	0.500	0.416
5	Capture probability	0.496	0.421	0.449	0.533	0.864	0.787	0.747	0.811	0.901		0.668
	Standard error	0.094	0.080	0.068	0.067	0.054	0.064	0.078	0.058	0.091		0.073
	Breeding probability	0.756	0.681	0.709	0.793	1.000	1.000	1.000	1.000	1.000		0.882
	Fecundity	0.378	0.341	0.355	0.397	0.500	0.500	0.500	0.500	0.500		0.441
6	Capture probability	0.742	0.724	0.576	0.644	0.855	0.895	0.741	0.740			0.740
	Standard error	0.063	0.049	0.050	0.049	0.049	0.036	0.083	0.092			0.059
	Breeding probability	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			1.000
	Fecundity	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500			0.500
7	Capture probability	0.742	0.724	0.576	0.644	0.855	0.895	0.741				
	Standard error	0.063	0.049	0.050	0.049	0.049	0.036	0.083				
	Breeding probability	1.000	1.000	1.000	1.000	1.000	1.000	1.000				
	Fecundity	0.500	0.500	0.500	0.500	0.500	0.500	0.500				
8	Capture probability	0.742	0.724	0.576	0.644	0.855	0.895					
	Standard error	0.063	0.049	0.050	0.049	0.049	0.036					
	Breeding probability	1.000	1.000	1.000	1.000	1.000	1.000					
	Fecundity	0.500	0.500	0.500	0.500	0.500	0.500					
9	Capture probability	0.742	0.724	0.576	0.644	0.855						
	Standard error	0.063	0.049	0.050	0.049	0.049						
	Breeding probability	1.000	1.000	1.000	1.000	1.000						
	Fecundity	0.500	0.500	0.500	0.500	0.500						
10	Capture probability	0.742	0.724	0.576	0.644							
	Standard error	0.063	0.049	0.050	0.049							
	Breeding probability	1.000	1.000	1.000	1.000							
	Fecundity	0.500	0.500	0.500	0.500							
11	Capture probability	0.742	0.724	0.576								
	Standard error	0.063	0.049	0.050								
	Breeding probability	1.000	1.000	1.000								
	Fecundity	0.500	0.500	0.500								
12	Capture probability	0.742	0.724									
	Standard error	0.063	0.049									
	Breeding probability	1.000	1.000									
	Fecundity	0.500	0.500									

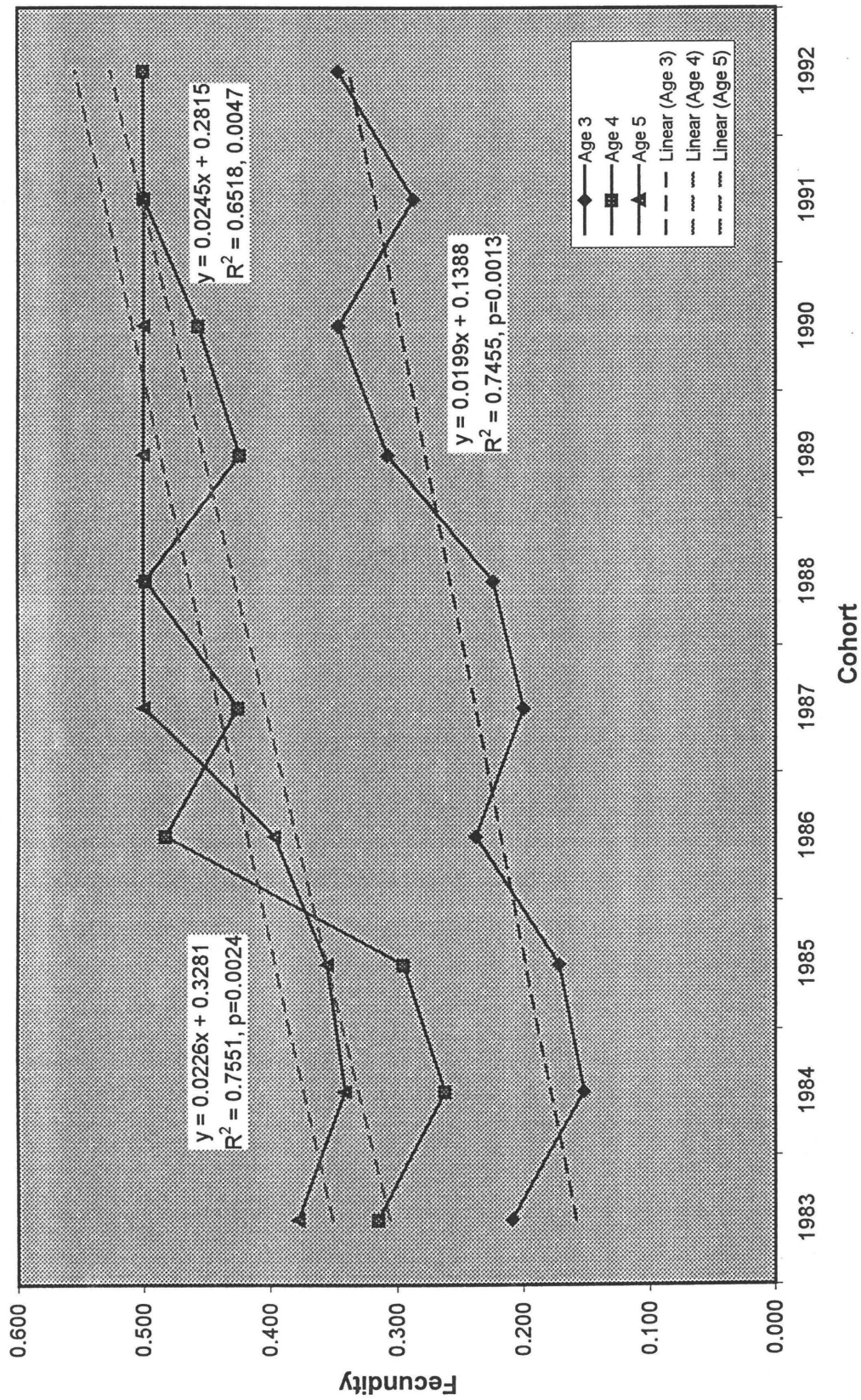


Figure 14. Inter-cohort comparison (1983-1992) of age-specific fecundity rates in southern elephant seals at Marion Island

5.4 Discussion

Although once considered a nuisance parameter, the capture rate, which is incorporated into Cormack-Jolly-Seber based survival models (Cormack 1964; Jolly 1965; Seber 1965), has recently been thought to bear some biological meaning (Cezilly *et al.* 1996). Clobert (1995) have, for example, shown how if only breeding birds are caught, differences in “catchability” reflect differences in their probability of breeding, whereas Testa *et al.* (1990) used sighting probability of Weddell seal females with pups as an index of reproductive rate. The present chapter made use, and demonstrated the applicability, of capture probabilities as a means of deriving reproductive parameters in elephant seals.

The fecundity rates determined in this chapter were high compared to that found in other pinniped studies (Croxall & Hiby 1983; Boyd 1985; Testa 1987; Huber *et al.* 1991; Boyd *et al.* 1995; Lima & Paez 1997). Despite the differences in methodology, the fecundity rates obtained in the present study from the 1983 cohort were, however, similar to that obtained by Wilkinson (1991) for the same cohort (8.1%, 3.9% & 0.01% higher respectively in the present study for three-, four- and five-year-olds).

The mean age of sexual maturity declined over the study period. This decline is likely to be a response to environmental changes since increased fecundity rates are expected when females are relieved from environmental stress (Caughley 1977). Changes in reproductive rates in large mammals have been observed as a response to both environmental changes (Gaillard *et al.* 1992; Lunn *et al.* 1994; Saether 1997) and changes in population density (Bowen *et al.* 1981; York 1983; Jorgenson *et al.* 1993). Population

density commonly influences demographic parameters since intraspecific competition reduces *per capita* food availability (Begon *et al.* 1990). Food availability influences body weight, and it is likely to explain to a large degree the variance in age at first reproduction in large mammals as well as providing a connection between ecological conditions and reproductive rates (Bengtson & Siniff 1981; Saether & Heim 1993). In many seasonally breeding mammals, a female's mass, unconstrained by her age, is a major component of whether or not she will give birth in a particular year (Saether & Haagenrud 1983; Gaillard *et al.* 1992; Saether 1997). In most Phocidae reproductive maturity is reached at a fairly constant proportion of adult body length, and is hence reached sooner when growth is accelerated (Laws 1956a). Assuming other conditions to remain unchanged, a decrease in population size may hence reduce intraspecific competition for food, increase *per capita* food availability, and this may in turn lead to increased growth rates and earlier maturation of animals (Bowen 1981; Choquenot 1991; Jorgenson *et al.* 1993).

The decrease in age of sexual maturity of elephant seals at Marion Island is therefore likely to be a consequence of a density dependent effect resulting from the decrease in numbers of seals during the study period. As the population number declined, an increase in prey per individual/unit area is expected, yielding a relative increase in available food resources. This would consequently be expected to give rise to a decrease in age of sexual maturity, due to a faster accumulation of body weight. A similar density dependent effect has been observed in northern elephant seals (Huber *et al.* 1991; Reiter & Le Boeuf 1991), harp seals (Bowen *et al.* 1981), bighorn ewes (Jorgenson *et al.* 1993), roe deer (Gaillard *et al.* 1992) and red deer (Saether 1997) with age of first reproduction being younger at low than at high population density.

Age-specific reproductive rates play a significant role in governing the rates of population change. After a given age breeding in elephant seals is regular with practically all the individuals breeding on an annual basis (Le Boeuf & Reiter 1988; Wilkinson 1991). The age at first reproduction, combined with the fecundity rates up to the age where all the females are recruited to the adult population, is therefore paramount in determining the reproductive output, and has a major influence on the dynamics of the population (Jorgenson *et al.* 1993). The increase in the proportion of females that are primiparous at age three, combined with the increase in fecundity of four- and five-year-old females (this study) are hence likely to have been proximately related to the slowing down of the population decline of southern elephant seals at Marion Island over the last few years (see section 6.3).

The present study lends further support to the hypothesis (*vide* Pascal (1980), Bester (1988) and Hindell (1991)) for a summary of hypotheses) that food as a limiting resource has been ultimately related to the population decline at Marion Island (chapter four). It is conceivable that food limitation gave rise to the population decline, and with the diminishing population size, *per capita* food availability has increased, which has consequently given rise to the decrease in age of maturity over the last ten years.

Fitness costs of early reproduction in terms of reduced future fecundity and survival has been observed for northern elephant seals (Huber 1987). Since 1983, survival of three-year-old female elephant seals at Marion Island have been declining at a rapid rate (chapter four). As an increase in the proportion of females in this age-category were observed breeding over the same time-period, the decrease in survival could, at least partially, be

implied as a fitness cost affecting early breeders. If this was the case, however, a similar decline in survival of four-year-olds would be expected due to the increase in fecundity. As this is not the case, the fitness cost argument seems unlikely.

It is reasonable to query the assumption made that a constant proportion of tagged females were sighted during the breeding seasons throughout the duration of the present study. With the reduction in the size of the harems, as a consequence of the population decline (S.P. Kirkman, unpublished results), a higher sighting rate (accounting for the increase in age-specific fecundity rates over time) might have been expected due to the relative ease with which females situated central to smaller harems were identified. If such an increase in sighting rate occurred due to the diminishing harem sizes, it would, however, have been reflected also in the capture probabilities of females aged six and older. Although these values signified a rather high level of variability, no positive trends were identified, as would have been the case if the proportion of tagged females that were identified increased over the study period. The variability in capture probability of females older than five years of age is, however, a weakness in the study as it contradicts the above-mentioned assumption. This presumably had a small effect on the fecundity rates that are representative of the entire study period, and more significantly affected the inter-cohort comparison of age-specific fecundity. The linear regressions in Fig. 14 showed a good fit to the data points and it therefore seems unlikely that the above mentioned variability accounted for the observed trends in fecundity rates.

The elephant seal population at Marion Island therefore appears to show density-dependent responses, with age of maturity decreasing as the population size declined. It is

speculated that the relative increase in food availability has given rise to a faster attainment of a critical body mass required for sexual reproduction, which consequently has led to a decrease in age of maturity.

CHAPTER 6 SIZE, STATUS & STANDING AGE-DISTRIBUTION

6.1 Introduction

Southern elephant seals were hunted extensively for their oil during the 18th and 19th centuries. By 1909 the sealing industry had virtually ended and protection was conferred upon most of the elephant seal populations (Laws 1994). These populations were thought to have recovered from the effects of overhunting by the 1950's (Carrick *et al.* 1962a). However, there have subsequently been reports of a decline in elephant seal numbers in several of the southern Indian and Pacific Ocean populations (Barrat & Mougine 1978; Condy 1978; Bester 1980; Skinner & Van Aarde 1983; Pascal 1985; Burton 1986; Hindell & Burton 1987; Guinet *et al.* 1992; Bester & Wilkinson 1994). Populations at sites in the South Atlantic have apparently remained stable (South Georgia, Gough Island) or are on the increase (Peninsula Valdes) (Bester 1990; Campagna & Lewis 1992; Campagna *et al.* 1993; Boyd *et al.* 1996).

Despite a 44% decrease in population size between 1956 and 1989, Iles Kerguelen is the only locality in the southern Indian Ocean that appears to have stabilized in recent years (Guinet *et al.* 1992), at a population size of around 143 500 (Laws 1994). The Heard

Island elephant seal population is estimated to have declined at an average rate of 2.4% annually since 1949, resulting in a 50% decline in numbers between 1949 and 1990, and a current population size of some 40 350 individuals (Burton 1986; Laws 1994). The Ile de la Possession (Iles Crozet) population has declined at 5.8% annually between 1966 and 1976, and at 5.7% per annum between 1980 and 1989 (Barrat & Mougín 1978; Guinet *et al.* 1992), resulting in a population of just over 2000 individuals in 1990 (SCAR 1991 in Laws 1994). The moulting population of elephant seals at the Vestfold Hills, Antarctica, which is part of the Heard-Kerguelen stock, has also declined by 50-75% since the late 1950's (Gales & Burton 1989). The population at Macquarie Island has declined at an average rate of 2.1% per annum between 1949 and 1984, with a net decrease of approximately 50% for that period (Hindell & Burton 1987). The population size was estimated at 86 500 individuals in 1985 (Hindell & Burton 1987).

Based on annual pup production, the Marion Island elephant seal population has declined at an average rate of 4.8% per annum from 1974 to 1989, but slowed to 1.9% per annum during the period 1983 to 1989 (Bester & Wilkinson 1994). The population size was estimated at 2009 individuals in 1990, a net decline of 83% since 1951, and 48.5% since 1976 (Laws 1994). The severity of this decline emphasizes the need to assess the present population size and the current rate of population decline, the subject of this chapter. The first standing age distribution, which gives the number of animals in each age class at a particular time, for a declining elephant seal population is also presented.

6.2 Methods

At any given time an unknown proportion of an elephant seal population is at sea and can not be counted. An indirect method of assessing population size is thus required. The number of pups produced annually is often used as an index of population size (Hindell & Burton 1987; McCann 1985; Wilkinson 1991). Pup production combined with the age structure of the population, can be used to estimate total population size (McCann 1985).

On the 15th of October, which is the peak haulout date for adult female elephant seals at all Indian Ocean breeding sites (Condy 1979; Wilkinson 1991), counts were made of all the adult females occupying breeding sites at Marion Island for the period 1986-1997. For each year at least two teams were involved to enable coverage of all the beaches in a single day. Counts were performed with a high level of reliability owing to the relatively small harems at Marion Island. As all, or nearly all, the females that haul out during the breeding season give birth to a single pup, counts of adult females are virtually equivalent to those of unweaned pups (McCann 1980; Pascal 1985; McCann & Rothery 1988). Based on the assumption that the number of adult females that are hauled out at this date represent 95% of those that haul out to breed (McCann 1985; Wilkinson 1991), a 5% correction factor was applied to the number of females hauled out on the 15th of October in order to derive pup production. The merit of this method is that it is much easier to count females directly than pups. Pups are often undercounted because of their small sizes, especially in larger harems.

For the period 1983 to 1990, the population declined at an exponential rate of 1.9% per annum (Bester & Wilkinson 1994), and as pup counts are only available since 1986, this estimate was used to derive pup production for 1983 to 1985. The population declined at an average rate of 4.8% per annum from 1974 to 1989 (Bester & Wilkinson 1994), and this estimate was used to derive the numbers of pups born in 1976 to 1982.

The standing age distribution, which gives the numbers of individuals in each age class at a particular time, relative to the number of individuals born in the same year (Caughley 1977), is estimated for the Marion Island elephant seal population for the period 1989 to 1992. It comprises animals born at the most recent birth pulse, one-year-olds of the cohort initiated at the previous birth pulse, two-year-olds of the cohort preceding that, and so forth. The l_x values from a stationary life table that is structured by using shot samples from a population, obtained at appropriate times, would give a direct representation of the age distribution of the population. For obvious reasons, such samples are not obtainable for the Marion Island elephant seal population, although cohort life tables for the years 1983-1992 are available (Appendix II) (for details on census methods, mark-recapture survival estimates and construction of these life tables see chapter four). For the 1991 standing age distribution, the l_x value for two-year-old seals was obtained from the 1989 cohort, that for three-year-olds from the 1988 cohort, etc. The problem with this approach lies in the fact that we are dealing with a declining population ($r < 0$). When employing the l_x value of two-year-olds from the 1989 cohort for the 1991 standing age distribution, it applies to the number of pups born in the 1991 birth pulse, which were less than the number of pups born in the 1987 birth pulse. The discrepancy would result in the number/proportion of two-year-olds present in 1991 being underestimated. To correct for this, respective l_x values

were multiplied by the pup numbers at the commencement of the relevant cohorts, to give the numbers of animals alive for each age category in 1991. The l_x values from the 1983 cohort life table were used for cohorts preceding that year. The number of seals alive in the respective age categories are added up to give the population size for that particular year. This total was then divided by the number of newborn pups to yield a conversion factor whereby annual pup production can be multiplied to estimate total population size.

The rate of population change was determined using the following exponential equation as in Caughley (1977):

$$r = (\ln N_t - \ln N_0)/t$$

where:

\ln = natural logarithm

N_t = population number at time t ,

N_0 = population number at the start of the period,

r = intrinsic rate of increase, and

t = time interval in years between the first and last observation,

as applied in other elephant seal population studies (van Aarde 1980; Bester & Lengart 1982; Vergani & Stanganelli 1990; Guinet *et al.* 1992).

In addition, a trajectory of pup production (which is an index to population size) was performed in order to assess the accuracy of the standing age-distributions. The means of the various parameters from the four standing age-distributions were used for the purpose of the trajectory, and is presented in a life-table for females. The following equation from Starfield & Bleloch (1991) was used for the trajectory:

$$k_{0,t+1} = \sum_{x=1}^{13} m_x p_{x-1} k_{x-1,t}$$

where $k_{0,t+1}$ = number of female pups born in the following year; m_x = the mean number of female offspring produced by a female that is x years old (chapter five); p_x = survival rates; and k_x = the number of females that are x years old. The rate of population change as deduced from pup production was compared to that predicted by the standing age-distribution.

6.3 Results

The estimates of annual pup production from 1986 to 1997 are shown in Table 24. From Tables 25 to 28 it can be calculated that the number of seals in the population of age one year and over was 3.10 times the annual pup production of 1989, 3.15 times that of 1990, 3.21 times that of 1991, and 3.18 times that of 1992. An appropriate conversion factor by which annual pup production can be multiplied to estimate total population size (excluding pups) for the Marion Island elephant seal population would therefore be the mean of the four values which is 3.15. Individuals of age 14 and older are not included in the standing

age distributions. Very few Marion Island elephant seals appear to reach such an age (only one sighted in 1997 out of 416 tagged in 1983), and it is assumed that they would have a negligible affect upon the value of the conversion.

By applying a 3.15 conversion factor, the 1997 population size (excluding pups), was estimated at 1326 individuals, and the 1986 population size at 2123 (Table 29). The population declined exponentially at an annual rate of 4.3%, and at a net rate of 37.5% from 1986 to 1997 (Fig. 15). During the first six years (1986 to 1992) the population declined at a rate of 5.9% per annum, but slowed to 2.5% per annum over the last six years (1991-1997). There was 16.3% less males than females in the 1989 standing age distribution, 16.4% less in 1990, 20.1% less in 1991, and 17.4% less in 1992. On average, there were 17.6% less males than females and the population is inferred to consist of approximately 60% females and 40% males.

A life table drawn up from the standing age distribution for females (1989-1992) is presented in Table 30, from which a trajectory of pup production predicted 237 individuals for the following year, yielding a 7.4% decline in pup production. This figure approximates the observed 5.9% decline in population size (1986-1992), and suggests a high level of reliability of the standing age-distributions.

Table 24. Annual pup production figures for Marion Island for the period 1986 to 1997, extrapolated from the number of cows counted on 15 October each year.

Year	Number of cows	Estimated pup production
1986	640	674
1987	599	631
1988	605	637
1989	547	576
1990	477	502
1991	467	492
1992	449	473
1993	454	478
1994	402	423
1995	428	451
1996	407	428
1997	400	421

Table 25. Standing age distribution of the Marion Island elephant seal population for 1989.

Age	Cohort	Pup numbers	<u>MALES</u>		<u>FEMALES</u>		Total
			l_x	Number	l_x	Number	
1	1988	637	0.618	197	0.603	192	389
2	1987	631	0.451	142	0.590	186	328
3	1986	674	0.353	119	0.455	153	272
4	1985	687	0.256	88	0.391	134	222
5	1984	700	0.143	50	0.211	74	124
6	1983	713	0.146	52	0.187	67	119
7	1982	747	0.109	41	0.133	50	91
8	1981	783	0.081	32	0.094	37	69
9	1980	821	0.075	31	0.067	28	59
10	1979	860	0.062	27	0.048	21	48
11	1978	901	0.041	18	0.034	15	33
12	1977	944	0.028	13	0.024	11	24
13	1976	985	0.000	0	0.017	8	8
Total				810		976	1786

Note: A sex ratio of 1:1 is assumed for pups.

Table 26. Standing age distribution of the Marion Island elephant seal population for 1990.

Age	Cohort	Pup numbers	<u>MALES</u>		<u>FEMALES</u>		Total
			l_x	Number	l_x	Number	
1	1989	576	0.550	158	0.616	177	335
2	1988	637	0.468	149	0.438	140	289
3	1987	631	0.341	108	0.404	127	235
4	1986	674	0.197	66	0.431	146	212
5	1985	687	0.149	51	0.245	84	135
6	1984	700	0.088	31	0.171	60	91
7	1983	713	0.109	39	0.133	47	86
8	1982	747	0.081	30	0.094	35	65
9	1981	783	0.075	29	0.067	26	55
10	1980	821	0.062	25	0.048	20	45
11	1979	860	0.041	18	0.034	15	33
12	1978	901	0.028	13	0.024	11	24
13	1977	944	0.000	0	0.017	8	8
Total				717		866	1583

Note: A sex ratio of 1:1 is assumed for pups.

Table 27. Standing age distribution of the Marion Island elephant seal population for 1991.

Age	Cohort	Pup numbers	<u>MALES</u>		<u>FEMALES</u>		Total
			l_x	Number	l_x	Number	
1	1990	502	0.607	152	0.664	167	319
2	1989	576	0.494	142	0.545	157	299
3	1988	637	0.349	111	0.351	112	223
4	1987	631	0.205	65	0.358	113	178
5	1986	674	0.172	58	0.316	107	165
6	1985	687	0.124	43	0.182	63	106
7	1984	700	0.045	16	0.146	51	67
8	1983	713	0.081	29	0.094	34	63
9	1982	747	0.075	28	0.067	25	53
10	1981	783	0.062	24	0.048	19	43
11	1980	821	0.041	17	0.034	14	31
12	1979	860	0.028	12	0.024	10	22
13	1978	901	0.000	0	0.017	8	8
Total				697		880	1577

Note: A sex ratio of 1:1 is assumed for pups.

Table 28. Standing age distribution of the Marion Island elephant seal population for 1992.

Age	Cohort	Pup numbers	<u>MALES</u>		<u>FEMALES</u>		Total
			l_x	Number	l_x	Number	
1	1991	492	0.601	148	0.642	158	304
2	1990	502	0.426	107	0.539	135	241
3	1989	576	0.427	123	0.390	112	235
4	1988	637	0.241	76	0.301	96	172
5	1987	631	0.177	56	0.262	82	138
6	1986	674	0.121	41	0.242	82	119
7	1985	687	0.108	37	0.132	45	74
8	1984	700	0.031	11	0.124	43	51
9	1983	713	0.075	27	0.067	24	37
10	1982	747	0.062	23	0.048	18	22
11	1981	783	0.041	16	0.034	13	7
12	1980	821	0.028	11	0.024	10	5
13	1979	860	0.000	0	0.017	7	7
Total				676		825	1502

Note: A sex ratio of 1:1 is assumed for pups.

Table 29. Estimates of the Marion Island elephant seal population size derived from annual pup production for the period 1986 to 1997.

Year	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997
Pup #	674	631	637	576	502	492	473	478	423	451	428	421
Popn	2123	1988	2007	1814	1581	1550	1490	1506	1332	1421	1348	1326

Table 30. Cross-sectional life table for female southern elephant seals from Marion Island. l_x values derived from standing age-distributions averaged over the period 1989-1992. Fecundity rates taken from chapter 5.

Age (x)	Frequency (f_x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)	Fecundity rate (m_x)
0	256	1.000	0.320	0.320	0.680	0.000
1	174	0.680	0.075	0.110	0.890	0.000
2	155	0.605	0.113	0.187	0.813	0.000
3	126	0.492	0.015	0.031	0.969	0.248
4	122	0.477	0.137	0.287	0.713	0.416
5	87	0.340	0.074	0.218	0.782	0.441
6	68	0.266	0.078	0.293	0.707	0.500
7	48	0.188	0.043	0.229	0.771	0.500
8	37	0.145	0.043	0.297	0.703	0.500
9	26	0.102	0.024	0.235	0.765	0.500
10	20	0.078	0.023	0.295	0.705	0.500
11	14	0.055	0.012	0.218	0.782	0.500
12	11	0.043	0.012	0.273	0.727	0.500
13	8	0.031				

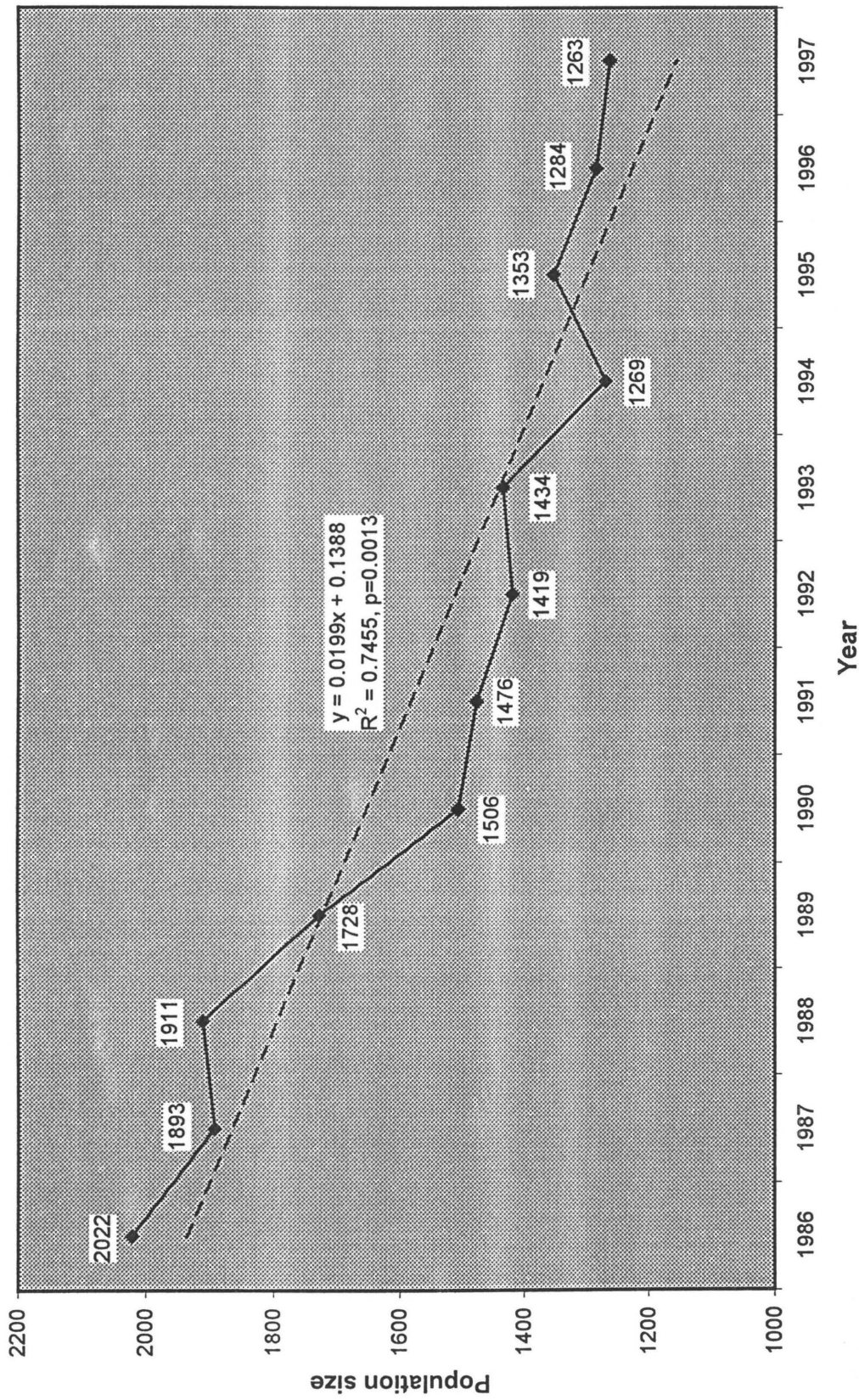


Figure 15. Estimates of the Marion Island elephant seal population size derived from annual pup production for the period 1986-1997.

6.4 Discussion

6.4.1 Population age-structure

Of the four previous studies on the dynamics of southern elephant seal populations (Laws 1960; McCann 1985; Hindell 1991; Wilkinson 1991), only that from South Georgia was cross sectional in nature and based on age structure data. Age structure data were derived from counts of dentine rings in the teeth of shot seals. Sample sizes were, however, well below that recommended by Caughley (1977), and it is questionable whether the age-classes derived from the exploited population were truly random (Hindell 1991). Studies by Hindell (1991) and Wilkinson (1991) on elephant seals from Macquarie Island and Marion Island respectively, were both based on mark-recapture data, from which cohort life tables were constructed. These would only have been representative of the age distributions of the two populations had their rates of change been zero (Caughley 1977). Thus, up to now there has been no published data dealing with the standing age distribution of a declining elephant seal population.

The standing age distribution of the Marion Island elephant seal population was calculated with the intention of estimating the total population size, and deriving a relationship between total population size and annual pup production. This will allow population numbers to be predicted when only pup numbers are available. The estimated conversion factor for the Marion Island population (3.15) is substantially lower than the figure of 3.5 estimated for the South Georgia population (McCann 1985). It has been recommended that different raising factors be applied to increasing, stable, or declining

populations (Laws 1994). Up to now, a conversion factor of 3.5 has been used for estimating abundance of southern elephant seal populations and to get an idea of the total population size (Laws 1994). Population abundance values have been used to estimate the biomass of various southern elephant seal populations and subsequently the annual prey consumption of these principal consumers of fish and squid in the southern ocean (Boyd *et al.* 1994; Condy 1981; Laws 1981; McCann 1985). The present study suggests that these should be reviewed.

A stationary life table of the stable South Georgia population (McCann 1985) indicates that there are some 20.8% less males than females in that population, an overall sex ratio that is comparable to the declining Marion Island population (17.6% less males than females). When taking only sexually mature animals of ages six to 12 years into account, the Marion Island population consists of 18% less males than females, and South Georgia, 44% less. This may be significant, as it suggests that at the declining Marion Island population, a substantially greater proportion of sexually mature animals are males than at the stable South Georgia population. Thus a greater proportion of sexually mature males on Marion Island are able to inseminate females than on South Georgia. This is in support of Bester & Wilkinson (1994) who discounted the hypothesis implicating the apparent paucity of males as a possible reason for the Marion Island elephant seal population decline (Skinner & van Aarde 1983).

Adult survival in large mammals is often sex-related with males suffering greater mortality rates than females (Roff & Bowen 1983; Toigo *et al.* 1997). This is particularly true for sexually dimorphic mammals (McCann 1985). The reason for this discrepancy in

survival has been ascribed to males being more susceptible to nutritional stress than females (Toigo *et al.* 1997), and may explain the larger proportion of females compared to males in the Marion Island elephant seal population (see Section 4.4.2).

6.4.2 Population size and rates of change

When employing the method used in this study for estimating population abundance, it is recommended that pup production be extrapolated from the numbers of adult females hauled out on a specific date, as opposed to counting pups directly. In the larger harems, many pups are concealed from observers, especially if there is no high vantage point overlooking the harem, and counts of females are likely to be far more dependable. An alternative method is to count the numbers of females, weaned pups and dead pups near the conclusion of the breeding season (end of October), as the three components together should represent total pup production (McCann 1985; Burton 1986; Hindell & Burton 1987; Wilkinson 1991). This is believed to provide a reliable estimate as (a) there are no new female arrivals at this stage (Wilkinson 1991), and (b) weaned pups have not yet departed from their natal beaches by this stage (Wilkinson & Bester 1990). However, this method requires that accurate records of pup mortality be kept throughout the breeding season (often an impracticable task), and is also subject to further potential inaccuracies: (a) females present may be the mothers of recently weaned pups or dead pups, that have not yet returned to sea, and could cause an overestimate, and (b) pups weaned earlier in the season may render themselves cryptic by this stage, by distancing themselves from the breeding area by either gathering in secluded localities marginal to the breeding area or

alternatively through movements into shallow water (Reiter *et al.* 1978; Lenglard & Bester 1982).

It is evident from the results that the Marion Island elephant seal population is still decreasing. It is cause for concern that the population has declined by at least 37.5% in the last generation. The rate of decline of the Marion Island population over the past decade is only surpassed by those of Iles Crozet, which has been declining at a rate of 5.7% per annum (Guinet *et al.* 1992), and Campbell Island (8.6% per annum) (Taylor & Taylor 1989). The rate of decline of the Marion Island population has diminished from the 4.8% per annum recorded for the years 1951 to 1989 (Wilkinson 1991), to 4.3% per annum for the years 1986 to 1997. During the current decade, it has slowed down even further to 2.5% per annum.

There appeared to be no substantial difference between the proportions of females in the population in the 1990-1992 age distributions. It seems that both sexes are declining at a similar rate although the sample size ($n=4$) is probably too small to draw any statistically meaningful conclusions.

Due to a similar rate of decline in elephant seal numbers in the southern Indian and southern Pacific oceans, Hindell & Burton (1987) concluded that there may be a common causative factor, or factors, contributing to it (see Hindell *et al.* 1994 for details). The South Atlantic populations appear to be either stable or increasing. Should it be that populations of the southern Indian and Pacific oceans are indeed subjected to similar regulating forces, they would be expected to have similar age structures. It is suggested

that future estimates of population abundance for all Indian and Pacific ocean southern elephant seal populations employ a conversion factor of 3.15 rather than the 3.5 which was previously used. Sensitivity analyses are yet to be used to determine the applicability of the new conversion factor to populations with different rates of growth (Pistorius *et al.* in revision).

With the apparent deceleration in the rate of population decline of Marion Island elephant seals, population size, and hence rate of decline for the following number of years needs to be ascertained. Considering the halt in the decline of the Iles Kerguelen elephant seal population, a similar pattern might be expected for the Marion Island population should similar causative factor(s) be responsible.

CHAPTER 7 CONCLUSIONS

The continued decline of elephant seal numbers at Marion Island was highlighted in this study. Based on a 3.15 conversion factor, which was derived from standing age-distributions for the population over four consecutive years, the population was estimated to consist of 2123 individuals in 1986, with a significant linear decrease to 1326 individuals in 1997. The population was therefore reduced by 37.5% during this period and experienced an exponential rate of decline of 4.3% per annum. Although these figures are rather staggering, when considering the decrease in the rate of decline to 2.5% per annum over the last six years, it seems that the pressure(s) on the population is/are lessening. This is furthermore substantiated by the equivalence of population size in 1994 and 1997.

A likelihood method, rather than a ratio estimator that has been used for most previous studies of tag loss in pinnipeds, was used to determine the rates at which tags are lost in the Marion Island elephant seal population. Although the average rate of tag loss for both sexes and all ages combined was only 2% per year, a strong increase with age was observed. It was estimated that 35% of males and 16% of females would lose both tags by age 15, requiring corrections to avoid bias of demographic studies based on these tagging data.

After corrections for tag loss were made, a relatively high juvenile and low adult survival for the Marion Island population was highlighted, with marked discrepancies in inter-sexual survival. The relatively high and consistent first year survival observed in this study argues against the notion that juvenile survival in large mammals is the key component to population status (Eberhardt & Siniff 1977; Eberhardt 1981). Population growth rate appears to be more sensitive to adult survival than to any other vital rate as suggested by Eberhardt (1985) and Toigo *et al.* (1997). The study also indicates that seals in their first year at Marion Island are either less sensitive to environmental fluctuations than the older age-categories, or that they were subject to different environmental conditions.

The comparatively low and decreasing adult survival, and in particular female survival, observed in the study appears to be the proximate factor responsible for the population decline at Marion Island. A decrease in survival rates for components of the population with high energetic demands, namely males undergoing secondary growth spurts, and females subject to physiological stress associated with pregnancy and lactation, were observed during the study period. Food limitation, as deduced from the above observations, appears to be the ultimate cause driving the population decline at Marion Island.

The probability of breeding increased with age up to six years of age, reflecting the progressive increase in the number of females attaining breeding status in the population. On average fecundity was comparatively high at 0.25 for three-year-olds, 0.42 for four-year-olds, and 0.44 for five-year-olds. The fecundity rates for all these age-categories

increased over the study period, suggesting a general decrease in age of sexual maturity as the population declined. It is reasoned that the decrease in population size reduced intraspecific competition for food and increased *per capita* food availability. This in turn gave rise to increased growth rates and hence earlier maturation of the females.

As it appears that the onset of sexual maturity in females of large mammal species is the demographic variable that first responds to resource limitation (Fowler 1987; Owen-Smith 1990), the continued monitoring of the elephant seal population at Marion Island is consequential in terms of providing an index to environmental changes in that region of the southern ocean. A future study that lies in the scope of the database used in the present study, and that would be of considerable interest in terms of developing life-history theories, may consider the consequences of early breeding for subsequent survival and reproduction.

If the Marion Island elephant seal population prove to have stabilised, as seems to be the case with the Iles Kerguelen population, a study in the near future that may also be of considerable interest will be the comparison of demographic parameters from the population while in a state of decline compared to when it has stabilised. This will allow for the direct assessment of the impact of the causative factor(s) responsible for the decline on population parameters.

SUMMARY

Rates of tag loss were estimated for Dalton Jumbo Rototags that were applied to each hind flipper of 5743 recently-weaned southern elephant seal pups on Marion Island from 1983 to 1993. A maximum likelihood method based on the resighting times of seals retaining one or two tags was used to estimate tag loss and test for effects of seal age and for differences between males and females. Although the average rate of single-tag loss for both sexes and all ages combined was low (2% per year), this belied a strong increase in tag loss with seal age that was more pronounced for males than females; annual single tag loss at age 14 was 10% in males and 5% in females. At these relatively high rates of loss, substantial fractions of seals (35% of males and 16% of females) would lose both tags by age 15, requiring corrections to avoid bias of demographic studies based on these tagging data. The likelihood method used has significant advantages over a ratio estimator that has been used for most previous studies of tag loss in pinnipeds.

The study also quantified both the age- and sex-specific survival rates of juveniles and adults, and tested for interannual differences in age-specific survival rates of the southern elephant seal population at Marion Island. Pups were tagged on an annual basis from 1983 onwards, and a consistent recapture program yielded data that was analysed using the software package MARK to obtain maximum likelihood estimates of survival and capture probability. On average first year survival was 0.58 and 0.62, and survival rate averaged over the first three years of life, 0.69 and 0.74 for males and females respectively. From years four to nine the average survival rate was 0.66 and 0.75 for males and females

respectively. Survival estimates for elephant seals in their 10th to 13th year are also presented, although these are based on very small sample sizes. Averages of age-specific survival estimates from the earlier (mostly 1983-1987 cohorts) and later (mostly 1988-1992 cohorts) periods were compared and considerable reductions were observed in fourth and fifth year male survival, and fourth year female survival. The decline in fourth year male survival was linear over the study period after adjacent survival estimates were averaged. The comparatively low adult survival is suggested as the proximate cause, and food limitation as deduced from the decline in survival of elephant seals with comparatively high energetic demands, as the ultimate cause behind the population decline at Marion Island. Although not tied in with the decline of the population, 1987, 1990 and 1993 were identified as high mortality years.

Age-specific fecundity rates for the population were derived from age-specific capture probabilities (incorporated into Cormack-Jolly-Seber based models) of females during the breeding season. On average fecundity was 0.25 for three-year-olds, 0.42 for four-year-olds, and 0.44 for five-year-olds. A significant increase in fecundity rate over the study period was evident for all the above age classes. It is speculated that the increased *per capita* food availability, resulting from the decline in elephant seal numbers, gave rise to a faster attainment of the minimum body weight required for sexual reproduction, and this consequently induced the observed changes in reproductive rates.

The population size at Marion Island was assessed using a combination of annual pup production and the standing age distribution for the population. The number of adult females hauled out on the 15th of October, which is the peak haul-out date for breeding

elephant seal females at all the Indian Ocean breeding sites, was used to extrapolate annual pup production for the period 1986 to 1997. The first standing age distribution for a declining elephant seal population is presented, and from this a conversion factor of 3.15 was determined by which annual pup production can be multiplied to yield population size. The present population size is estimated at 1263 individuals (excluding pups), and the population declined exponentially at an annual rate of 4.3%, and a net rate of 37.5%, from 1986 to 1997. The rate of decline slowed to 2.5% per annum over the last six years.

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APPENDIX I

Table 1. Pup mortality in southern elephant seals on Marion Island.

Year	1990	1991	1992	1993	1994	1995	1996	Average
Dead pups	18	16	13	14	21	33	14	18
Estimated pup production	502	492	473	478	423	451	428	464
Pup mortality	3.59%	3.25%	2.75%	2.93%	4.96%	7.32%	3.27%	4.01%

APPENDIX II

Table 1. Life table for male southern elephant seals tagged in 1983 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.349	0.349	0.651
1	0.651	0.189	0.290	0.710
2	0.462	0.115	0.248	0.752
3	0.348	0.101	0.292	0.708
4	0.246	0.071	0.287	0.713
5	0.175	0.030	0.170	0.830
6	0.146	0.037	0.252	0.748
7	0.109	0.028	0.253	0.747
8	0.081	0.006	0.074	0.926
9	0.075	0.013	0.179	0.821
10	0.062	0.021	0.336	0.664
11	0.041	0.013	0.328	0.672
12	0.028	0.028	1.000	0.000
13	0.000			

Table 2. Life table for female southern elephant seals tagged in 1983 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.353	0.353	0.647
1	0.647	0.177	0.273	0.727
2	0.470	0.056	0.119	0.881
3	0.414	0.135	0.326	0.674
4	0.279	0.024	0.085	0.915
5	0.256	0.068	0.268	0.732
6	0.187	0.054	0.290	0.710
7	0.133	0.039	0.290	0.710
8	0.094	0.027	0.290	0.710
9	0.067	0.019	0.290	0.710
10	0.048	0.014	0.290	0.710
11	0.034	0.010	0.290	0.710
12	0.024	0.007	0.290	0.710
13	0.017			

Table 3. Life table for male southern elephant seals tagged in 1984 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.395	0.395	0.605
1	0.605	0.203	0.336	0.664
2	0.402	0.181	0.451	0.549
3	0.221	0.052	0.236	0.764
4	0.168	0.026	0.153	0.847
5	0.143	0.055	0.382	0.618
6	0.088	0.043	0.485	0.515
7	0.045	0.014	0.318	0.682
8	0.031	0.005	0.161	0.839
9	0.026	0.004	0.161	0.839
10	0.022	0.004	0.161	0.839
11	0.018	0.003	0.161	0.839
12	0.015			

Table 4. Life table for female southern elephant seals tagged in 1984 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.455	0.455	0.545
1	0.545	0.100	0.183	0.817
2	0.445	0.145	0.325	0.675
3	0.301	0.047	0.156	0.844
4	0.254	0.043	0.169	0.831
5	0.211	0.040	0.188	0.812
6	0.171	0.026	0.149	0.851
7	0.146	0.022	0.149	0.851
8	0.124	0.018	0.149	0.851
9	0.105	0.016	0.149	0.851
10	0.090	0.013	0.149	0.851
11	0.076	0.011	0.149	0.851
12	0.065			

Table 5. Life table for male southern elephant seals tagged in 1985 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.356	0.356	0.644
1	0.644	0.189	0.294	0.706
2	0.455	0.129	0.283	0.717
3	0.326	0.070	0.216	0.784
4	0.256	0.106	0.416	0.584
5	0.149	0.025	0.167	0.833
6	0.124	0.017	0.133	0.867
7	0.108	0.055	0.507	0.493
8	0.053	0.025	0.470	0.530
9	0.028	0.013	0.470	0.530
10	0.015	0.007	0.470	0.530
11	0.008			

Table 6. Life table for female southern elephant seals tagged in 1985 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.355	0.355	0.645
1	0.645	0.136	0.211	0.789
2	0.509	0.088	0.172	0.828
3	0.421	0.031	0.073	0.927
4	0.391	0.146	0.374	0.626
5	0.245	0.062	0.255	0.745
6	0.182	0.050	0.274	0.726
7	0.132	0.036	0.274	0.726
8	0.096	0.026	0.274	0.726
9	0.070	0.019	0.274	0.726
10	0.051	0.014	0.274	0.726
11	0.037			

Table 7. Life table for male southern elephant seals tagged in 1986 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.416	0.416	0.584
1	0.584	0.112	0.192	0.808
2	0.472	0.119	0.252	0.748
3	0.353	0.156	0.441	0.559
4	0.197	0.025	0.129	0.871
5	0.172	0.051	0.294	0.706
6	0.121	0.050	0.416	0.584
7	0.071	0.028	0.395	0.605
8	0.043	0.025	0.575	0.425
9	0.018	0.010	0.575	0.425
10	0.008			

Table 8. Life table for female southern elephant seals tagged in 1986 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.297	0.297	0.703
1	0.703	0.169	0.241	0.759
2	0.534	0.078	0.147	0.853
3	0.455	0.024	0.052	0.948
4	0.431	0.116	0.268	0.732
5	0.316	0.074	0.235	0.765
6	0.242	0.065	0.268	0.732
7	0.177	0.047	0.268	0.732
8	0.129	0.035	0.268	0.732
9	0.095	0.025	0.268	0.732
10	0.069			

Table 9. Life table for male southern elephant seals tagged in 1987 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.431	0.431	0.569
1	0.569	0.118	0.208	0.792
2	0.451	0.110	0.244	0.756
3	0.341	0.135	0.397	0.603
4	0.205	0.029	0.139	0.861
5	0.177	0.069	0.391	0.609
6	0.108	0.047	0.436	0.564
7	0.061	0.003	0.044	0.956
8	0.058	0.046	0.789	0.211
9	0.012			

Table 10. Life table for female southern elephant seals tagged in 1987 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.344	0.344	0.656
1	0.656	0.066	0.101	0.899
2	0.590	0.186	0.315	0.685
3	0.404	0.046	0.115	0.885
4	0.358	0.096	0.268	0.732
5	0.262	0.075	0.288	0.712
6	0.186	0.062	0.333	0.667
7	0.124	0.041	0.333	0.667
8	0.083	0.028	0.333	0.667
9	0.055			

Table 11.Life table for male southern elephant seals tagged in 1988 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.382	0.382	0.618
1	0.618	0.150	0.243	0.757
2	0.468	0.119	0.255	0.745
3	0.349	0.107	0.308	0.692
4	0.241	0.085	0.351	0.649
5	0.157	0.040	0.254	0.746
6	0.117	0.038	0.329	0.671
7	0.078	0.000	0.000	1.000
8	0.078			

Table 12.Life table for female southern elephant seals tagged in 1988 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.397	0.397	0.603
1	0.603	0.165	0.273	0.727
2	0.438	0.088	0.200	0.800
3	0.351	0.050	0.143	0.857
4	0.301	0.105	0.348	0.652
5	0.196	0.044	0.226	0.774
6	0.152	0.016	0.107	0.893
7	0.135	0.026	0.195	0.805
8	0.109			

Table 13.Life table for male southern elephant seals tagged in 1989 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.450	0.450	0.550
1	0.550	0.056	0.102	0.898
2	0.494	0.067	0.135	0.865
3	0.427	0.243	0.568	0.432
4	0.185	0.068	0.371	0.629
5	0.116	0.013	0.112	0.888
6	0.103	0.009	0.083	0.917
7	0.095			

Table 14.Life table for female southern elephant seals tagged in 1989 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.384	0.384	0.616
1	0.616	0.071	0.116	0.884
2	0.545	0.155	0.284	0.716
3	0.390	0.136	0.349	0.651
4	0.254	0.068	0.268	0.732
5	0.186	0.069	0.374	0.626
6	0.116	0.015	0.133	0.867
7	0.101			

Table 15.Life table for male southern elephant seals tagged in 1990 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.393	0.393	0.607
1	0.607	0.181	0.299	0.701
2	0.426	0.110	0.259	0.741
3	0.315	0.085	0.270	0.730
4	0.230	0.086	0.372	0.628
5	0.145	0.036	0.246	0.754
6	0.109			

Table 16.Life table for female southern elephant seals tagged in 1990 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.336	0.336	0.664
1	0.664	0.124	0.187	0.813
2	0.540	0.133	0.246	0.754
3	0.407	0.091	0.223	0.777
4	0.316	0.050	0.159	0.841
5	0.266	0.028	0.105	0.895
6	0.238			

Table 17.Life table for male southern elephant seals tagged in 1991 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.399	0.399	0.601
1	0.601	0.162	0.270	0.730
2	0.439	0.099	0.225	0.775
3	0.340	0.155	0.457	0.543
4	0.185	0.046	0.248	0.752
5	0.139			

Table 18.Life table for female southern elephant seals tagged in 1991 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.358	0.358	0.642
1	0.642	0.123	0.192	0.808
2	0.519	0.091	0.176	0.824
3	0.427	0.118	0.276	0.724
4	0.309	0.038	0.124	0.876
5	0.271			

Table 19.Life table for male southern elephant seals tagged in 1992 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.570	0.570	0.430
1	0.430	0.096	0.223	0.777
2	0.334	0.077	0.231	0.769
3	0.257	0.117	0.455	0.545
4	0.140			

Table 20.Life table for female southern elephant seals tagged in 1992 at Marion Island.

Age (x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	1.000	0.442	0.442	0.558
1	0.558	0.087	0.156	0.844
2	0.471	0.089	0.189	0.811
3	0.382	0.073	0.191	0.809
4	0.309			