

Growth of the southern elephant seal

***Mirounga leonina* (Linnaeus 1758) at Macquarie Island.**

by

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Declaration

I hereby declare that this thesis contains no material which has been accepted for the award of any degree or diploma in any university or institution, and that to the best of my knowledge, this thesis contains material solely by the author except where due acknowledgement has been made.

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Abstract

Body growth was an essential component of early biological research undertaken to develop sustainable harvesting methods of the southern elephant seal (*Mirounga leonina* Linnaeus 1758). Since slaughter ceased in most areas earlier this century, a substantial decline in numbers of elephant seals has been recognised at several of the main breeding sites, stimulating interest in life-history attributes which may help provide an explanation for these declines. Growth of elephant seals from the Macquarie Island population was investigated to quantify the current growth pattern and to compare with the stable population at South Georgia, where elephant seals were known to be larger, grow faster, and breed earlier.

A method was developed to indirectly measure body mass using photogrammetry. Predictive models were developed using photographic images alone, but when compared with models based on measured morphological characteristics, the best predictor of body mass was a combination of body length and girth squared.

Growth during the first foraging trip was described and found to reflect the hindrances of early life at sea. Growth was hypothesised to comprise primarily of adjustment to body composition, rather than increase in net body size. Both sexes may exploit similar marine resources during the first foraging trip, as no significant difference in body growth was found. Interspecific comparison suggested that southern elephant seals grow considerably more than northern elephant seals (*M.*

angustirostris) during this period, and that this may be related to prey abundance and distribution.

A cross-sectional growth study was undertaken for females up to 15 years of age. Dental cementum layers were counted to estimate the age of some animals, which proved to be a relatively accurate and useful technique. The snout-tail length of adult Macquarie Island cows has increased significantly since the 1950s and 1960s, and is now similar to that of the current South Georgia population. The temporal changes at in snout-tail length at Macquarie Island are consistent with either a population equilibration process or long-term environmental change reducing population density. These findings provide little supporting evidence for a particular cause of the Macquarie Island population decline, but the most likely scenario is that several factors are implicated, these having resulted in changes in marine resource availability.

Body growth of southern elephant seals is determined by many factors, but prey abundance and distribution are fundamental influences on all growth stages. Other factors which may play a role include harem disturbances, behaviour of weaners, disease, juvenile body size and stored energy reserves.

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CHAPTER ONE

INTRODUCTION.

The southern elephant seal (*Mirounga leonina* Linnaeus 1758), is the largest pinniped and one of the most sexually dimorphic of all mammals (King 1983; Le Boeuf and Laws 1994). Capable of diving to over 1500 m depth and for up to 120 minutes, they dive longer and deeper than other pinnipeds (Hindell *et al.* 1991a; McConnell and Fedak 1996). Travelling over 2000 km to reach foraging grounds, southern elephant seals have been estimated to travel up to 130 km per day, spending 10 months of every year at sea (Hindell *et al.* 1991b; McConnell *et al.* 1992; Fedak *et al.* 1994). Whilst at sea, they spend 90% of their time submerged, with only minutes at the surface between dives (Hindell *et al.* 1991a; McConnell and Fedak 1996). Such biological characteristics allow southern elephant seals to have a major impact on prey species in the Southern Ocean, with estimates of approximately 5.6 million tonnes of squid and 1.8 million tonnes of fish being consumed per annum by the total population (McCann 1985). The predominantly oceanic existence of southern elephant seals however, makes scientific studies difficult to undertake.

Breeding from September and November on subantarctic islands, females spend approximately 4 weeks ashore giving birth and lactating; males may remain ashore for up to 8 weeks (Ling and Bryden 1981). Females and males then spend a further 3 to 4 and 8 to 9 weeks respectively, ashore between January and April whilst

moulting (Laws 1960a; Hindell and Burton 1988a). During these haul-out periods, southern elephant seals fast completely, utilising energy stores in their bodies that have accumulated whilst foraging at sea (Slip *et al.* 1992a; Boyd *et al.* 1993; Hindell *et al.* 1994a).

Southern elephant seals were slaughtered for over 100 years at all major breeding sites, with in excess of one million individuals estimated to have been taken (Laws 1994). They were sought after for high quality oil derived from their blubber, and were taken in an uncontrolled manner. At Macquarie Island, they were taken between 1810 and the early 1900s without any form of regulation (Hindell and Burton 1988b), however at South Georgia, government control of sealing began in 1910. Commercial harvesting continued at South Georgia until the late 1960s (Headland 1984).

It was not until 1948 though, that any research was undertaken when at South Georgia and Signy Island, a 3 year project was initiated to develop a sustainable harvesting method (Laws 1960a). Although this study covered many aspects of southern elephant seal biology, one area of particular interest was growth (Laws 1953). An understanding of growth of this species would “provide a scientific basis for its exploitation and control” (Laws 1960a). Research studies of southern elephant seal growth at Macquarie Island were also undertaken with harvesting in mind. Carrick and Ingham (1962a) noted that such research was necessary prior to commercial slaughter of a wild species. Bryden (1967) undertook a more detailed study to understand body compositional changes of southern elephant seals at

Macquarie Island, and attempted to relate this to domesticated, food-producing animals (Bryden 1969a). Since commercial slaughter of elephant seals ceased at all breeding sites, a substantial decline in numbers has been reported in several of the major populations (Hindell and Burton 1987). Consequently, much interest has developed in studying life history variables which may explain or at least, indicate reasons for such a decline.

This study aims to investigate growth of southern elephant seals at Macquarie Island in an attempt to quantify the current growth pattern of animals during their first foraging trip and for females over their life-time. Quantifying and describing growth may enable comprehension of the adaptive process that juvenile southern elephant seals undergo to survive in the marine environment. Subsequent growth and mature body size attained may provide further information on southern elephant seal population ecology, and could provide clues for the cause of the population decline.

1.1 The genus.

The genus name *Mirounga* is derived from ‘miouroung’, an Australian Aboriginal name (Le Boeuf and Laws 1994). The second species of the genus, *M. angustirostris*, or northern elephant seal, is very similar in size, appearance, behaviour and diving ability to the southern species (Le Boeuf and Laws 1994). The northern species is characterised by a more pendulous proboscis in males, is found in subtropical areas along the west coast of North America and is less able to assume a U-shaped body posture (Ling and Bryden 1992). Considerable genetic differences

are believed to exist between the two species as a result of the northern elephant seal population experiencing an extreme population bottleneck and developing genetic homogeneity (Bonnell and Selander 1974; Hoelzel *et al.* 1993). Southern elephant seals in contrast, have a considerable degree of genetic variation (Gales *et al.* 1989).

1.2 Distribution of southern elephant seals.

Southern elephant seals have a circumpolar distribution in the southern hemisphere (Figure 1.1). Laws (1960a) defined three independent breeding populations: (i) the southern Pacific Ocean stock, breeding mainly on Macquarie Island and to a lesser extent on Campbell Island; (ii) the southern Indian Ocean stock, breeding mainly on Îles Kerguelen and Crozet, Heard, Marion and Prince Edward Islands; (iii) the southern Atlantic Ocean stock breeding mainly in the Scotia arc (*i.e.* South Georgia, South Orkney, South Shetland, and South Sandwich Islands), the Falkland Islands and Península Valdés on the Argentinean coast. Regular haul-outs of moulting non-breeding animals, predominantly males, have also been recorded on the Antarctic coast at the Vestfold Hills and the Windmill Islands (Burton 1985; Gales and Burton 1989).

1.3 Status of southern elephant seals.

The current estimation of the world population of southern elephant seals (1 year or older) is 664 000, with the southern Atlantic, southern Indian Ocean and southern Pacific Ocean stocks estimated to contain 397 000, 189 000 and 78 000 seals

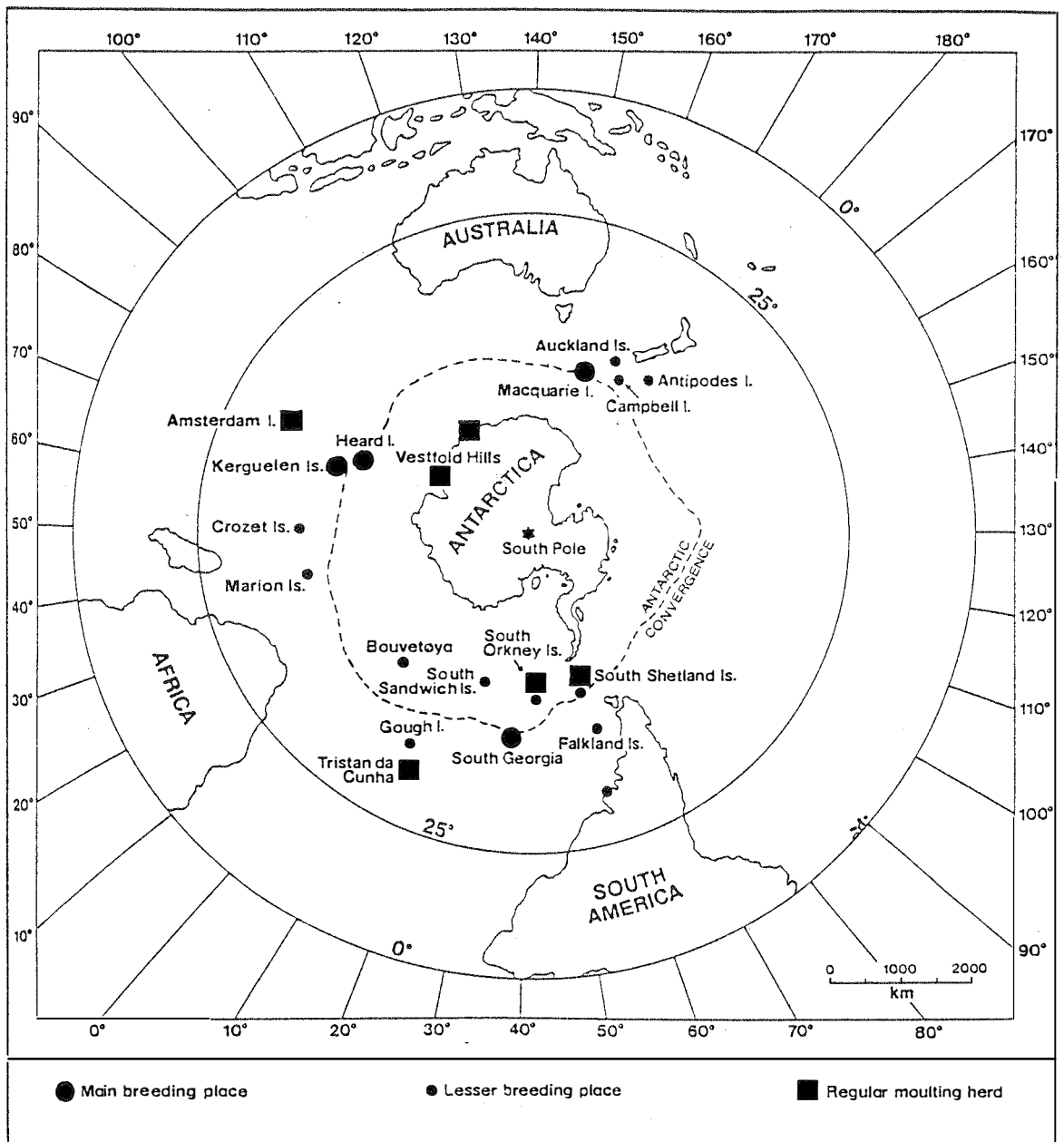


Figure 1.1. The distribution of southern elephant seals, showing breeding and moulting sites (from Bryden 1993). The main breeding populations are divided into the southern Pacific, the southern Indian Ocean, and the southern Atlantic Ocean islands.

respectively (Laws 1994). There have been substantial declines reported in several of the main breeding populations, in particular the southern Indian and Pacific Ocean stocks (Hindell *et al.* 1994b). In contrast, the southern Atlantic Ocean stock appears to be stable (Boyd *et al.* 1996) and the population at Península Valdés increasing (Campagna and Lewis 1992).

1.4 Life-time growth of southern elephant seals and life history.

A complete study of growth of any mammal involves the growth of the foetus, however such studies are uncommon for pinnipeds (*e.g.* Trites 1991). By accelerating prenatal growth, instead of extending the gestation period as large terrestrial mammals do (*e.g.* 22 months for elephants (Laws 1981)), pinnipeds are able to produce a relatively large foetus (Laws 1959). Implantation of the blastocyst in southern elephant seals is delayed after fertilisation for a period of approximately 4 months (Laws 1956a), with foetal mass then undergoing an exponential increase over the 7 month period of foetal growth (Laws 1956a; Bryden 1969b; Ling and Bryden 1981). Body length in contrast, tends to increase in a linear fashion (Bryden 1969b; McLaren and Smith 1985). Trites (1991) described foetal growth (body length specific) of northern fur seals (*Callorhinus ursinus*) and suggested that significant intersex differences begin shortly after implantation and increase through to birth. He proposed that male foetuses weigh more because their skeletons are longer (hence greater mass can potentially be accumulated). Male southern elephant seal pups are born approximately 14% heavier than females, reflecting greater maternal expenditure on male offspring during gestation (Arnbom *et al.* 1994).

Members of the Phocidae family (earless seals) are generally characterised by a short suckling period with rapid pup growth during this time (Laws 1959). Southern elephant seal pups are born during September to November into large harems of cows. At birth, pups weigh approximately 40 kg (Condy 1980; Guinet 1991; Campagna *et al.* 1992; Hindell *et al.* 1994c). Whilst suckling, pups undergo a pronounced dynamic change, trebling their body weight over the 23 day nursing period (Carrick *et al.* 1962a). A large percentage of this increase results from deposition of adipose tissue in the form of subcutaneous blubber (Bryden 1969c). Newborn southern elephant seals are born with as little as 3% fat at birth, increasing to approximately 40% at weaning, whilst lean tissue mass changes very little until the last four days of the lactation period (Hindell *et al.* 1994c). The rapid development of blubber prior to weaning is important as it acts as an energy store and thermo-insulation (Bryden 1964), both being critical for the survival of an animal that is yet to learn how to swim and forage properly.

This period of rapid growth is in direct contrast with the ensuing postweaning fast which lasts between 3 to 9 weeks (Ling and Bryden 1981; Arnborn *et al.* 1993). Weaned pups move out of the crowded harem and congregate away from adult animals. Although growth curves of fat, muscle and viscera are reversed during the fast, positive growth of bone continues, suggesting that both fat and muscle are metabolised (Bryden 1969c). Bone growth is believed to continue positively because of the effect of gravity and the need for a stable structure to house internal organs and enable muscle attachment (Bryden 1969c). The fast may also be an important

developmental stage for behaviour, social skills and diving physiology (Arnbom *et al.* 1993; Modig 1995).

The loss of 30% of the weaning mass generally coincides with departure from the natal site and commencement of the first foraging trip (Wilkinson and Bester 1990; Arnbom *et al.* 1993). Pups must rapidly and proficiently adapt to aquatic life without maternal guidance, so that they can travel large distances, forage, and avoid predators such as killer whales (*Orcinus orca*) (Ling and Bryden 1981). Further, individuals must undergo catch-up growth to compensate for energy reserves lost during the fast. Little is known about this phase of life when a large percentage of animals do not survive (Hindell and Burton 1987; Hindell 1991). Only now are diet and foraging behaviour being elucidated (Green and Burton 1993; Slip 1995; Slip *in press*).

Growth continues over the next few years in a negative exponential fashion for females, accelerating steadily from the beginning of the second year of life, to approximately 3 to 4 years (McLaren 1993). At this age, males and virgin females are not easily distinguished (Carrick *et al.* 1962a). Annual increments in body mass and length of females then decline, with females reaching approximately 2.5 m body length and 400 to 600 kg body weight at growth maturity (Ling and Bryden 1981; Fedak *et al.* 1994). Males undergo a sigmoid pattern of growth (McLaren 1993), with a secondary period of accelerating growth at 6 to 7 years of age, coinciding with puberty (Carrick *et al.* 1962a). Males may not reach breeding status until at least 10 years of age at Macquarie Island (Carrick *et al.* 1962a; Jones 1981), at

which bulls can weigh up to 3700 kg and measure more than 5.0 m in body length (Ling and Bryden 1981). Males of the South Georgia population were believed to start breeding at a younger age and smaller body size, possibly the result of commercial activities selectively removing older larger males from that population (Laws 1960b). The growth pattern of males may account for the extreme sexual dimorphism observed in this species (Ling and Bryden 1981).

Advantages of increased body size in male elephant seals are two fold. Large body size allows for greater energy stores available for haul-out periods (McCann 1981). Increased size also confers dominance characteristics, such that larger males are higher ranking and consequently, have a higher copulatory frequency and hence, greater reproductive success (McCann 1981; Modig 1996). Larger southern elephant seal males of higher dominance rank also remain ashore for longer periods when compared to lower ranking males (Modig 1996). Similar effects of size on dominance rank and energy stores have been recorded for northern elephant seal bulls (Deutsch *et al.* 1990; Haley *et al.* 1994).

During haul-outs to breed and moult, cows expend energy stored whilst foraging at sea. The size of mothers is an important influence on pup size at both birth and weaning (Arnbom *et al.* 1993; Arnbom *et al.* 1994). A minimum post-partum body mass of 300 kg must be achieved before female southern elephant seals can maintain a pregnancy, presumably related to energy stores available for lactation and foetal growth (Arnbom *et al.* 1994). Smaller cows may utilise a greater percentage of their fat stores than larger cows when producing a pup, but both small and large cows

may often be missing in subsequent breeding seasons, suggesting that both body sizes could be restricted physiologically (Arnbom *et al.* 1994; Fedak *et al.* 1996).

1.5 Growth studies of southern elephant seals.

Differences have previously been recorded for growth patterns of elephant seals at South Georgia and Macquarie Island (Figure 1.2), with the Macquarie Island population believed to have a slower growth rate, increased age at first breeding and smaller adult body size (Carrick *et al.* 1962a; Bryden 1968a). Currently, there is indirect evidence to suggest that the difference in growth rate between the two sites has reduced (Arnbom *et al.* 1994; Hindell *et al.* 1994a; Hindell and Slip *in press*).

The first intensive growth study of southern elephant seals was performed by Laws (1953) at South Georgia, directly measuring 226 individual animals up to 17 years of age. The age of these animals was determined by counts of dentine layers from collected canine teeth (Laws 1953). Carrick *et al.* (1962a) undertook a study of growth at Macquarie Island, using a total of 83 direct measurements from animals up to 8 years of age. This study utilised known-age subjects, as it was part of a long-term mark-resight program (Carrick and Ingham 1962a). Ninety-six animals of up to 17 years of age were directly measured in a subsequent study at Macquarie Island by Bryden (1967), using similar age determination techniques as Laws (1953). The studies of Laws (1953) and Carrick *et al.* (1962a) also included numerous indirect measurements, using photogrammetric and visual estimations respectively.

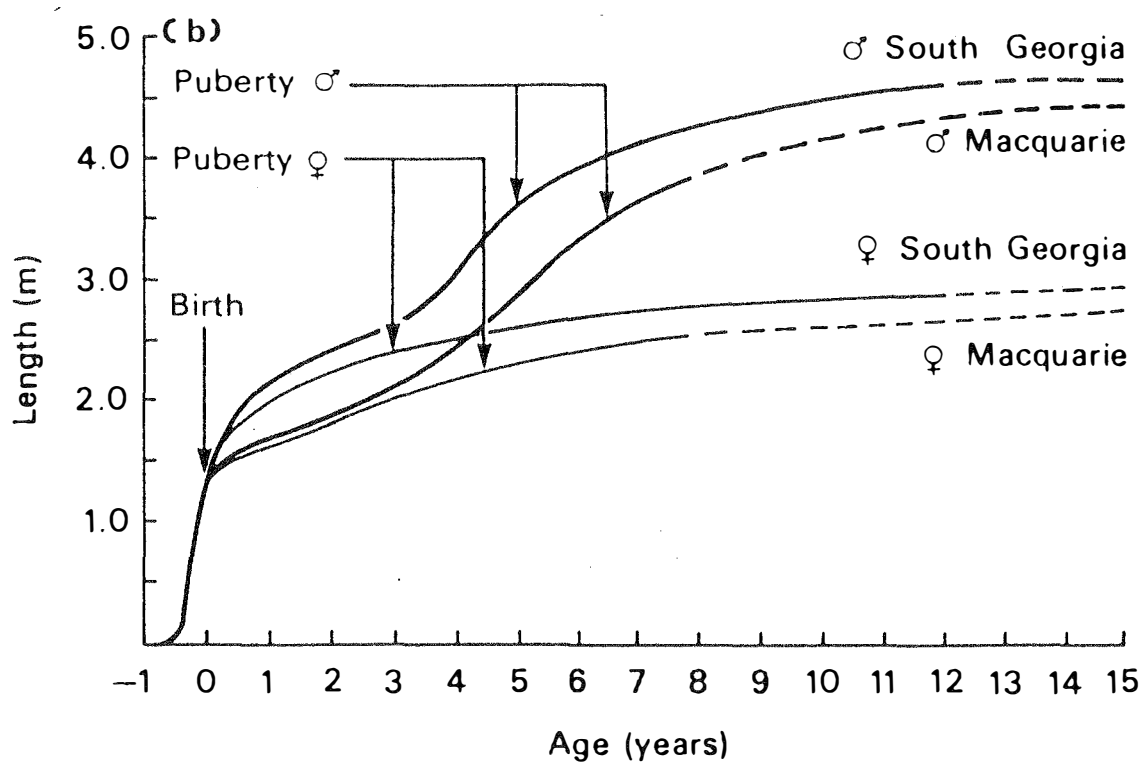


Figure 1.2. Straight-line body length growth curves for the southern elephant seal at Macquarie Island (1950s and 1960s) and South Georgia (1948-51) (from Laws 1984).

1.6 Why study growth?

Body growth analysis has many implications for the ecology of mammals. It can provide an objective criterion for monitoring physiological condition of mammalian populations (Hanks 1981), indicate prey abundance (Trites and Bigg 1992), highlight foraging success and body condition of mothers (Crête *et al.* 1993), and measure nutritional status (Reimers 1972; Mitchell *et al.* 1976). In general, slower growing individuals within a species or population tend to have reduced survivorship (Choquenot 1991; Lee *et al.* 1991). Environmental factors may also play a role in limiting the genetic growth potential of mammals (*e.g.* Suttie and Hamilton 1983).

The recognition of substantial population declines of southern elephant seals during the last 30 to 40 years in the south Pacific and Indian Oceans has been the stimulus for recent research activities (Hindell *et al.* 1994b). Although many single factors have been suggested as the cause, it is more likely to be multifactorial (Hindell *et al.* 1994b). Factors such as density dependent pup mortality, predation, increased fishery activity, and competition with other vertebrate consumers for food resources seem unlikely to be the inciting cause of the decline (Hindell and Burton 1987; Hindell 1991; Hindell *et al.* 1994b). The two current explanations are: (i) *the environmental change hypothesis* where fluctuations in the ocean environment are implicated in having an impact on food species used by southern elephant seals (Burton 1986; Hindell *et al.* 1994b), and (ii) *the equilibration hypothesis* where equilibration processes after a population “overshoot” are proposed to be a direct

result of heavy exploitation of elephant seals since the eighteenth century (Hindell *et al.* 1994b).

The environmental change hypothesis predicts that first-year survival should change markedly in a nondirectional manner over short periods of time (Hindell *et al.* 1994b), if responding to short-term environmental change such as an El Niño event (Fairbach *et al.* 1991). Longer term environmental change, such as global warming (Folland *et al.* 1984; Jones *et al.* 1986), would presumably be reflected by more gradual and directional demographic changes. However, the effects of such changes would depend on the type of effect they have on prey species. If overall prey availability was reduced, then the resulting population decline could have a density-dependent effect, allowing for increased prey availability per capita, as suggested for the northern fur seal population on the Pribilof Islands between 1958 and 1974 (Trites and Bigg 1992). This increase in prey per capita could be reflected in positive changes such as increased adult body size and earlier onset of first breeding for females. On the other hand, if long-term changes resulted in decreased prey availability and caloric density, then changes such as reduced adult body size and later onset of first breeding for females may result (Hanks 1981; Stewart and Lavigne 1984). The equilibration hypothesis predicts that with stabilisation of the population, adult and first year survival will increase directionally, somatic growth rates will increase and adult body size will increase, but age at first breeding for females will decrease (Hindell *et al.* 1994b). By undertaking growth studies of southern elephant seals, predictions of these hypotheses pertaining to growth rate

and adult body size can be tested. Indirectly, growth studies may also test predictions relating to age at first breeding and first year foraging success.

Today, cross-sectional studies involving the slaughter of large numbers of seals are generally not undertaken. Instead mark-resight studies (*e.g.* Bester 1988) are used to obtain data pertaining to growth. At Macquarie Island, elephant seals have been regularly marked using plastic flipper tags since 1987, and now large numbers of weaned pups have been permanently identified by hot-iron brands annually since 1993 (H. Burton *pers. com.*). Permanent identification of large numbers of known-age animals provides a useful data set of individuals, especially considering the high site-fidelity of southern elephant seals (Nicholls 1970; Lewis *et al.* 1997).

1.7 Aims and structure of the study.

By examining the growth of southern elephant seals at Macquarie Island, this study aims to address the following fundamental questions:

- what is the current growth pattern of southern elephant seals of the Macquarie Island population?
- what factors determine growth?
- has growth of the Macquarie Island population changed since the 1950s and 1960s?
- does growth of elephant seals at Macquarie Island differ from the South Georgia population (or at least from the 1950s when earlier studies were conducted)?

Field work for this study was undertaken in the isthmus study area (Carrick *et al.* 1962b) on Macquarie Island (54° 30' S, 158° 57' E) between March 1994 and January 1995 (Figure 1.3).

The thesis has 3 data chapters which are based on separate papers that are either in press (Chapter 2; Bell *et al. in press*) or in preparation for submission (Chapters 3 and 4). As the chapters have been prepared in this way, there is some repetition in the Methods sections.

The aim of Chapter 2 was to determine a suitable direct or indirect method of estimating body mass and other morphometrics for use in growth studies.

Chapter 3 focuses on growth in the first year of life, using known-age animals. This study is unique in that it utilises permanently identified animals from the current mark-recapture program and is the first to examine growth of elephant seals in their first year of life, particularly during the first foraging trip.

Chapter 4 aims to quantify the current life-time growth pattern of females (inadequate data was collected for males to achieve the same objective), to address observations that Macquarie Island cows are smaller, breed later and grow slower than South Georgia counterparts. This chapter uses a combination of known-age animals, as well as animals aged using dental cementum layers. This is a method of age determination widely used for marine mammals, as well as other terrestrial mammals. Retrospective analysis of data from the 1950s and 1960s from Macquarie

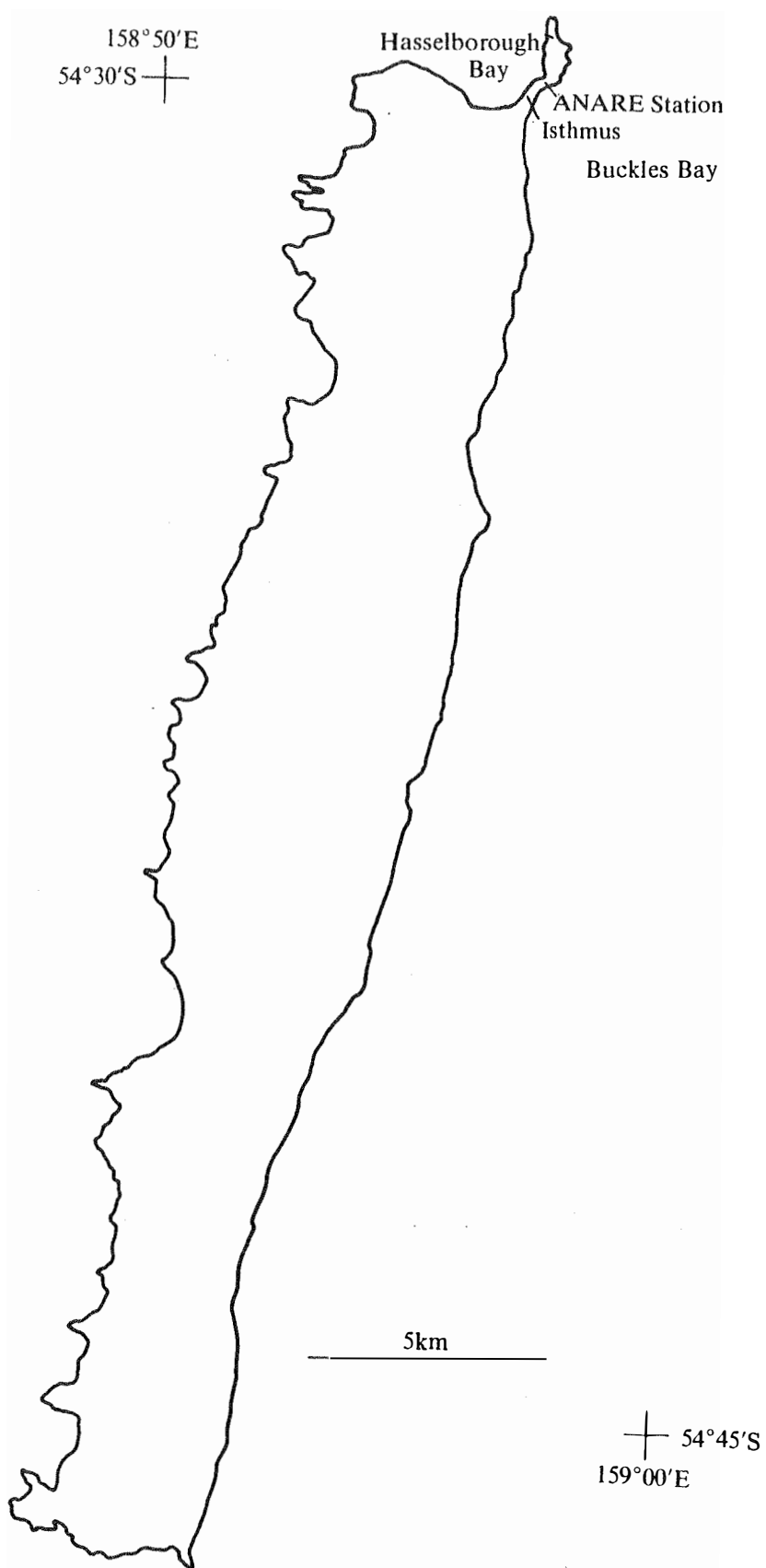


Figure 1.3. Map of Macquarie Island (after Selkirk *et al.* 1990).

Island also provides temporal comparison and may provide some explanation for the current decline of this population.

Chapter 5 is a general discussion of the findings, and relates these to seal ecology and population dynamics. It presents an overview of factors which may be implicated in affecting growth of southern elephant seals.

CHAPTER TWO

INDIRECT AND DIRECT METHODS OF ESTIMATING MORPHOLOGICAL CHARACTERISTICS.

2.1 Introduction.

Direct measurement of the mass of large phocids is difficult and potentially dangerous for both biologists and specimens. Further, transporting heavy weighing equipment can be extremely awkward in field situations (Boyd *et al.* 1993), whilst weighing large numbers of phocids can be time consuming and physically demanding (Arnbom *et al.* 1993). However, data such as body masses are necessary to assess the condition of phocid seals and must be obtained despite these problems.

Photogrammetry, the science of making measurements on photographs (Baker 1960), is now a well established technique used in a wide range of fields including geology, agriculture, medicine and mapping (Atkinson 1980). Specialised equipment is available which extends the usefulness of the technique (Karara 1979). Laws (1953) first utilised a photographic technique for marine mammals to estimate body length of southern elephant seals. More recently, aerial photography has been used in cetaceans, including southern right whales (*Eubalaena australis*), fin whales (*Balaenoptera physalus*), and bowhead whales (*Balaena mysticetus*), as a means of making indirect morphological measurements (Cubbage and Calambokidis 1987; Best 1992; Ratnaswamy and Winn 1993). Terrestrial photogrammetry was used to predict body mass of northern elephant seal bulls from photographically measured

variables (Haley *et al.* 1991) and more recently, southern elephant seal cows at South Georgia (Modig 1995).

The aim of this chapter is to develop an indirect method of estimating body mass of southern elephant seals using both digital photogrammetry and morphometrics, to overcome the logistical problems associated with direct mass estimation.

2.2 Methods.

Field work was undertaken at the isthmus study area (Carrick *et al.* 1962b) of Macquarie Island during 1994 and 1995. A total of 95 animals were weighed and photographed. This sample consisted of 36 yearlings (between 5 and 15 months of age; 19 male, 17 female), 32 immature individuals (18 male, 14 female) and 27 post-lactation cows. The immature animals were non-breeding males and females. Adult bulls were not included in this study because of labour and equipment constraints.

Individual animals were sedated prior to photographing. Most animals less than 2 years of age were physically restrained with a canvas head-bag and sedated by intravenous injection of approximately 0.9 mg/kg of ketamine hydrochloride and 0.03 mg/kg of diazepam (see Slip and Woods 1996). All other animals were sedated using a 1:1 mixture of tiletamine and zolazepam at a dose of 1 mg/kg (Baker *et al.* 1990), administered intramuscularly by a remote injection method (Ryding 1982).

2.2.1 Photographic measurement.

Initially, a Nikon 35mm SLR, connected to a Kodak DSC200 charged couple device (CCD) that converts light to digital signals, was utilised. This was fitted with a 28mm focal length lens, which provided a coverage similar to a 80 mm lens due to a small sensor area. Later, a Canon ION 260 video-still camera was used. Despite reduced image quality, this unit proved to be considerably more practical due to its smaller size, robustness and ease of use.

Once immobilised, two images were obtained of each animal; a side and front view (see Haley *et al.* 1991). Side views were taken from a distance of approximately 4.5 metres, with the camera 0.3 metres above the ground. Frontal pictures were taken with the camera at a similar height, but approximately 2.5 metres from the snout of the seal. A calibration pole, with a red and white 100 millimetre scale, was held by an assistant over the midline for side pictures and over the axillae, at right angles to the midline, for front views. Photographs were taken at the point of maximum inspiration to standardise the side area estimates which varied with the respiratory cycle. Seals were only photographed when lying on packed sand or hard ground, and when their body could be positioned in a straight line.

2.2.2 Field measurements.

Mass was determined to the nearest kilogram by suspending the seal in a stretcher underneath an aluminium tripod using electronic strain gauge scales of 2500kg capacity of ± 1 kg accuracy (Measurement Systems International, Seattle, Washington, USA). Snout-tail length (STL) and axillary girth (G) (Table 2.1) were

Table 2.1. Variables, abbreviations and units used in models. Variable-type refers to either photographic (P) or morphological (M) variables.

Variable	Variable-type	Abbreviation	Units
Side area	P	SA	m ²
Girth area	P	GA	m ²
Side perimeter	P	SP	m
Girth perimeter	P	GP	m
Snout to base of hind flippers	P	L	m
Volume	P	VOL	m ³
Snout to tail length	M	STL	m
Axillary girth	M	G	m
Body mass	M	M	kg
Body height ^a	P	H	m

^a Taken at various locations along the length of the body. Refer to Figure 2.1 for specific positions.

measured with the animal in ventral recumbency (American Society of Mammalogists 1967) with a plastic tape-measure.

2.2.3 Calculations.

Once downloaded to a computer, the digital images were preprocessed and enhanced with an image analysis program (Aldus Photostyler 2.0, Aldus Corporation, Seattle, 1994) to eliminate orthogonal linear distortion caused by the scanning/downloading process (A. Vrana, *pers. comm.*). The image file was transmitted via a satellite link to Australia and imported into a commercial computer aided design (CAD) program (AutoCAD Release 12, Autodesk, Inc., Sausalito, 1992) as a screen overlay file. The outline of both side and frontal images were then manually traced with a digitiser. The caudal flippers were disregarded in the side image tracing as their position was variable. Using the calibration pole in the original image, the scale of the tracing entity could be adjusted accordingly by the ratio of real length : digitised length.

Quantitative data were obtained for the following photographic variables (also defined in Table 2.1): (i) side area (SA, equivalent to the area of a longitudinal section taken at the midline) (ii) girth area (GA, equivalent to the area of a cross section at the axillary girth) (iii) body length (L, Figure 2.1) (iv) side height (H, see below and Figure 2.1) (v) side perimeter (SP, perimeter of side section) and (vi) girth perimeter (GP, perimeter of girth section). All variables were measured using S.I. units. As the position of the tail was obscured by the caudal flippers in photographs, the straightline measurement (L) of snout to the base of hind flippers

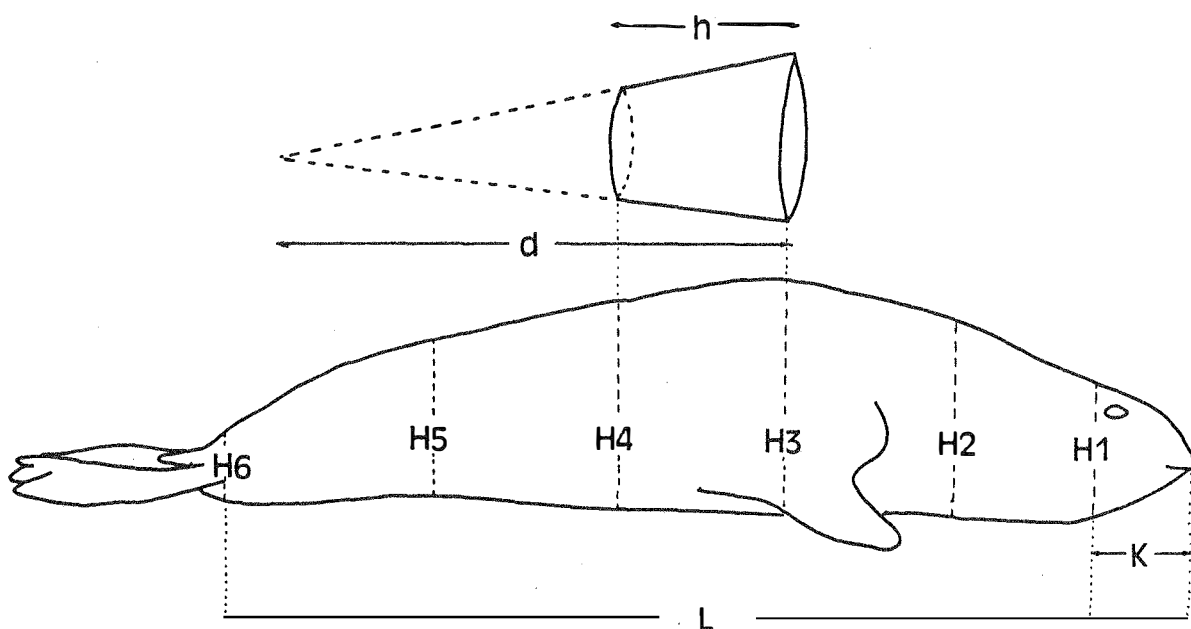


Figure 2.1. Diagrammatic representation of height measurements (H1 to H6) made from the side view. L represents the snout to base of hind flipper length estimated from the digital image. The anteriormost height measurement (H1) was at the straightline distance (K) from the snout: 0.2 m in seals up to one year of age or 0.3 m in seals greater than 1 year of age. H3 represented the height at the axillary girth and H6 the height at the base of the hind flippers. The remaining height measurements were made at equal intervals according to the diagram. The two other variables used for each truncated cone were the height of the section (h), and the height of the 'parent' cone (d).

(where the caudal flippers meet the body) was made, as per Haley *et al.* (1991). Four replicate measurements were made for each variable. The mean of these 4 measurements was used in the derivation of regression equations. Heights were also measured at 6 locations along the length of the side images (Figure 2.1) to enable the estimation of a body volume.

The method of Gales and Burton (1987) was modified to estimate the volume of seals. This assumed that individuals were circular in cross-section, such that the diameter for any cross-section was equivalent to the side height at that point. To perform the calculations, each animal was divided into five sections which were treated as five truncated cones, each with ends of diameters corresponding to the two sets of adjacent height measurements (Figure 2.1). The head and hind flipper section were disregarded in the calculations as these were minimal in terms of volume and difficult to estimate. Each section was treated as a separate truncated cone to calculate the total volume. For each of these, the end with the greater height was treated as the base and the other end as a parallel section of a cone. The height (h) of the sections was calculated by subtracting K (straightline distance from the snout to H1) from the length (L), estimated from the side image, and dividing by five (Figure 2.1). Volumes were calculated for the 'parent' cone (cone^a) containing each section (base radius = height for the base/2, cone height = d) and the smaller apical subcone (cone^b) (base radius = height of shorter section end/2, height = $d-h$). See Figure 2.1. The total volume of the section was then deduced by subtracting the

volume of cone^b from cone^a (refer to Appendix 1 for calculation details). The sum of the volumes of all five sections was the total estimated volume for the seal.

2.2.4 Data analysis.

Regression analysis of body mass on all combinations of the photographic and morphometric variables (Table 2.1) was performed, in the form of log-log linear and power models. Adjusted multiple r-squared values (r^2) were derived for these single and multiple regressions. Colinearity was recognised as a potential cause of spurious r^2 values (Zar 1984), as a high degree of intercorrelation existed between many of the independent variables in the multiple regressions. To overcome colinearity, data from 13 individuals, randomly selected from the total pool ($n = 95$), were used as test cases to assess the predictability of different models. Data from these individuals were not used in the derivation of models. This group was composed of 5 yearlings (3 male, 2 female), 5 post-lactation cows, and 3 immature animals (2 male, 1 female). These numbers were selected so that adequate sample sizes remained to derive models. Only class-specific test cases were used to trial class-specific models. Confidence intervals (C.I.) of 95% for the mean percentage difference between the real mass and model predicted mass, that is, the percentage that the real mass was of the predicted mass, were estimated from these test cases. As a measure of reliability of models, confidence intervals instead of r^2 values were used.

2.3 Results.

Many equations were obtained using different combinations of photographic and/or morphometric variables. The best fifteen models selected on the basis of the 95% confidence interval for each of the three groups are presented here: (i) all individuals combined (Table 2.2) (ii) post-lactation cows (Table 2.3) and (iii) yearlings (Table 2.4). Models were further divided into those with (i) photographic variables only (ii) morphometric variables only and (iii) a combination of photographic and morphometric variables. The standard error for replicate measurements of photographic variables, as a percentage of the mean, was estimated for each animal. Mean error was less than 0.7%, with a maximum of 3.9% for SP.

2.3.1 Class non-specific.

The best confidence interval, $\pm 3.91\%$, (model 6, Table 2.2) was for the power model which contained the morphometric variables STL and G (Figure 2.2). For models with only photographic variables, the best confidence interval was $\pm 4.71\%$ (model 1, Table 2.2), taking into account SA and GA. The most useful and best correlated photographic variable was SA (model 4, Table 2.2, Figure 2.3). As expected from geometrical relationships, body mass was found to be proportional to approximately $(\text{length})^3$ (model 9, Table 2.2) and volume (*unpub. data*). For completeness, confidence intervals are also presented for these models when tested using class-specific test cases (Table 2.2).

Table 2.2. Models for mass estimation, 95% confidence intervals (95% C.I.) for the percentage difference between predicted and real body mass, and coefficients of determination (r^2) derived from a combination of yearlings, post-lactation cows and other animals (as outlined in text). $n = 13$ for estimation of the 95% confidence intervals (non-specific). 95% C.I. are also shown for the models when test cases were used specific to the post-lactation cow ($n = 5$) and yearling ($n = 5$) classes.

#	Model	r^2	n	95% C.I. (non-specific)	95% C.I. (cows)	95% C.I. (yearlings)
<i>Photographic variables only</i>						
1	$M = 849.288(GA^{0.462})(SA^{1.071})$	0.983	45	4.71	2.92	16.15
2	$M = 15.543(GP^{2.491})(SP^{0.443})(GA^{-0.700})(SA^{0.658})$	0.987	45	5.58	4.26	14.99
3	$M = 21.045(GP^{1.757})(SP^{1.054})$	0.984	45	5.74	4.68	14.49
4	$LOG_e M = 6.176 + 1.454(LOG_e SA)$	0.939	79	6.36	8.42	15.95
5	$M = 612.859(SA^{0.697})(GA^{0.571})(L^{0.462})$	0.984	45	6.45	4.16	15.77
<i>Morphometric variable only</i>						
6	$M = 53.896(STL^{1.063})(G^{1.697})$	0.991	82	3.91	2.17	6.16
7	$LOG_e M = 3.630 + 2.523(LOG_e STL)$	0.902	81	5.59	6.89	7.24
8	$LOG_e M = 4.269 + 2.795(LOG_e G)$	0.958	82	6.43	4.72	6.35
9	$M = 31.259(STL^{2.772})$	0.842	82	6.57	6.80	7.42
10	$M = 81.827(G^{2.543})$	0.964	82	7.06	4.37	6.02
<i>Combination of photographic and morphometric variables</i>						
11	$M = 89.185(VOL^{0.168})(STL^{0.953})(G^{1.428})$	0.993	58	4.42	2.53	7.06
12	$M = 121.929(SA^{0.644})(GP^{1.033})(STL^{0.629})$	0.987	43	4.70	2.66	12.50
13	$M = 111.447(GP^{0.381})(SP^{-0.235})(GA^{-0.008})(SA^{0.392})(STL^{0.827})(G^{1.015})(L^{0.086})$	0.994	49	4.73	1.96	8.06
14	$M = 196.498(SA^{0.772})(G^{1.341})$	0.987	48	4.85	2.76	10.61
15	$M = 26.541(SP^{1.022})(G^{1.699})$	0.988	82	5.84	4.30	10.37

Table 2.3. Models for mass estimation, 95% confidence intervals (95% C.I.) for the percentage difference between predicted and real body mass, and coefficients of determination (r^2) for post-lactation cows. $n = 5$ for estimation of the 95% confidence intervals.

#	Model	95% C.I.	r^2	n
<i>Photographic variables only</i>				
16	$M = 332.136(\text{VOL}^{0.594})(L^{1.074})$	8.02	0.901	18
17	$M = 124.535(\text{VOL}^{0.570})(\text{SP}^{1.161})$	8.02	0.902	18
18	$M = 478.332(\text{SA}^{1.542})$	8.35	0.862	22
19	$M = 323.737(\text{SA}^{1.344})(L^{0.399})$	8.71	0.869	22
20	$\text{LOG}_e M = 6.139 + 1.421(\text{LOG}_e \text{SA})$	8.76	0.829	21
<i>Morphometric variables only</i>				
21	$M = 69.540(\text{STL}^{0.629})(G^{1.942})$	3.22	0.938	22
22	$M = 99.353(G^{2.304})$	5.14	0.840	22
23	$\text{LOG}_e M = 4.621 + 2.253(\text{LOG}_e G)$	5.24	0.742	22
24	$M = 29.778(\text{STL}^{2.709})$	7.09	0.624	22
25	$\text{LOG}_e M = 3.756 + 2.294(\text{LOG}_e \text{STL})$	7.80	0.586	21
<i>Combination of photographic and morphometric variables</i>				
26	$M = 125.331(\text{SA}^{0.550})(\text{STL}^{0.492})(G^{1.299})$	2.66	0.963	22
27	$M = 127.373(\text{VOL}^{0.249})(\text{STL}^{0.800})(G^{1.219})$	3.04	0.965	17
28	$M = 178.484(\text{SA}^{0.600})(G^{1.481})$	3.32	0.955	22
29	$M = 34.467(\text{SP}^{0.754})(G^{1.775})$	4.95	0.951	22
30	$M = 193.284(\text{VOL}^{0.223})(G^{1.706})$	5.16	0.942	17

Table 2.4. Models for mass estimation, 95% confidence intervals (95% C.I.) for the percentage difference between predicted and real body mass, and coefficients of determination (r^2) for yearlings. $n = 5$ for estimation of the 95% confidence intervals.

#	Model	95% C.I.	r^2	n
<i>Photographic variables only</i>				
31	$M = 37.801 + (699.639 \cdot H5)$	9.22	0.569	21
32	$\text{LOG}_e M = 4.133 + 2.393(\text{LOG}_e GP)$	13.14	0.796	22
33	$M = 56.681(GP^{2.681})$	13.22	0.883	23
34	$M = -101.022 + (782.382 \cdot H4)$	13.31	0.691	21
35	$M = 1030.753(H4^{1.700})$	13.37	0.708	21
<i>Morphometric variables only</i>				
36	$M = 51.114(STL^{1.076})(G^{1.793})$	6.22	0.967	29
37	$M = 74.239(G^{2.566})$	6.58	0.942	30
38	$\text{LOG}_e M = 4.324 + 2.501(\text{LOG}_e G)$	6.63	0.911	31
39	$M = 32.21(STL^{2.851})$	6.86	0.793	31
40	$\text{LOG}_e M = 3.591 + 2.572(\text{LOG}_e STL)$	7.28	0.784	31
<i>Combination of photographic and morphometric variables</i>				
41	$M = 778.488(GP^{0.281})(SP^{-2.474})(GA^{-0.006})(SA^{0.511})(STL^{1.144})(G^{1.216})(L^{1.648})$	5.92	0.973	22
42	$M = 109.311(GA^{0.161})(G^{2.271})$	6.86	0.940	23
43	$M = 55.555(GP^{0.731})(SP^{-0.297})(GA^{-0.227})(SA^{0.291})(STL^{1.042})(G^{1.248})$	7.00	0.971	22
44	$M = 148.642(VOL^{0.307})(STL^{0.892})(G^{0.894})$	8.48	0.931	21
45	$M = 127.166(SA^{0.421})(G^{1.856})$	8.63	0.953	29

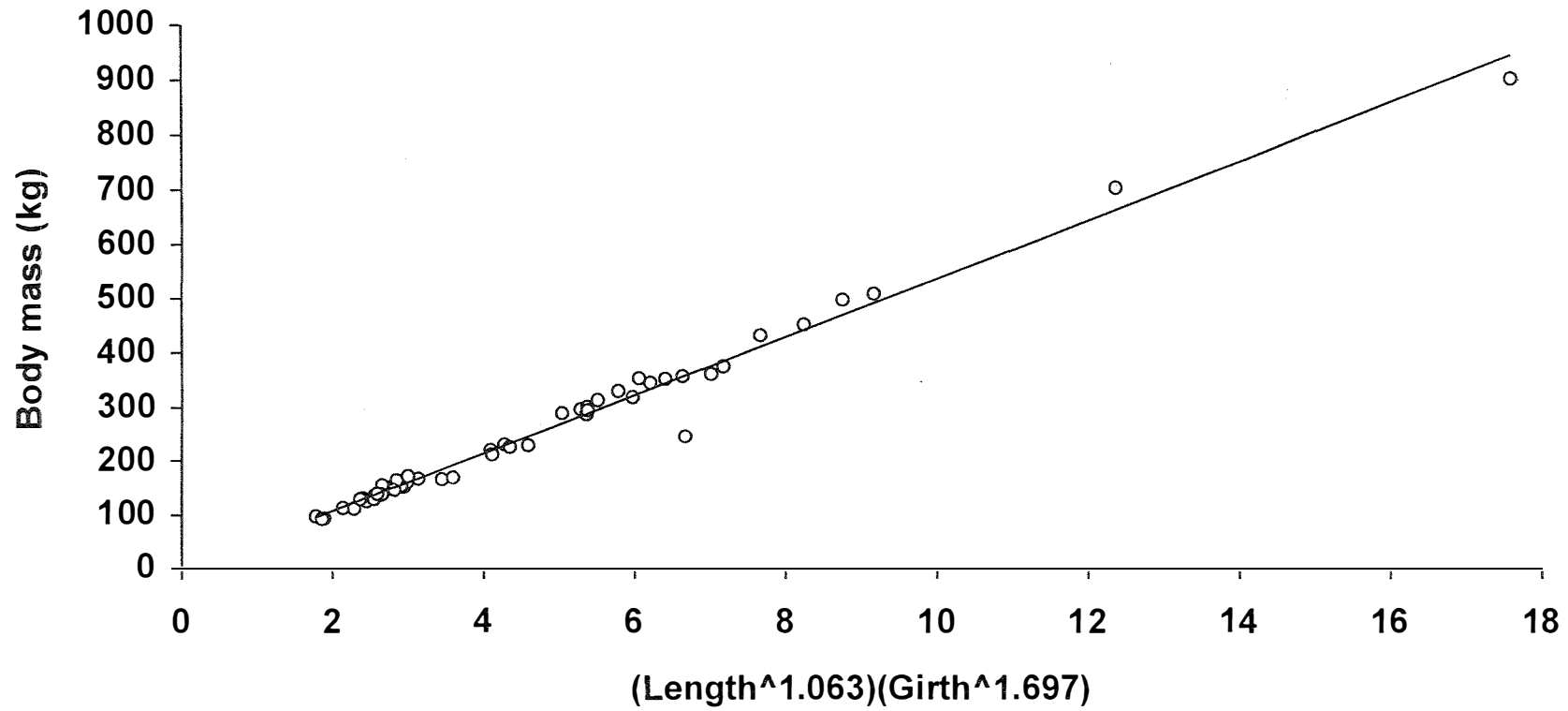


Figure 2.2. The relationship between body mass and snout-tail length/girth for model #6. $M = 53.896(STL^{1.063})(G^{1.697})$; $r^2 = 0.991$; 95% confidence interval ± 3.91 .

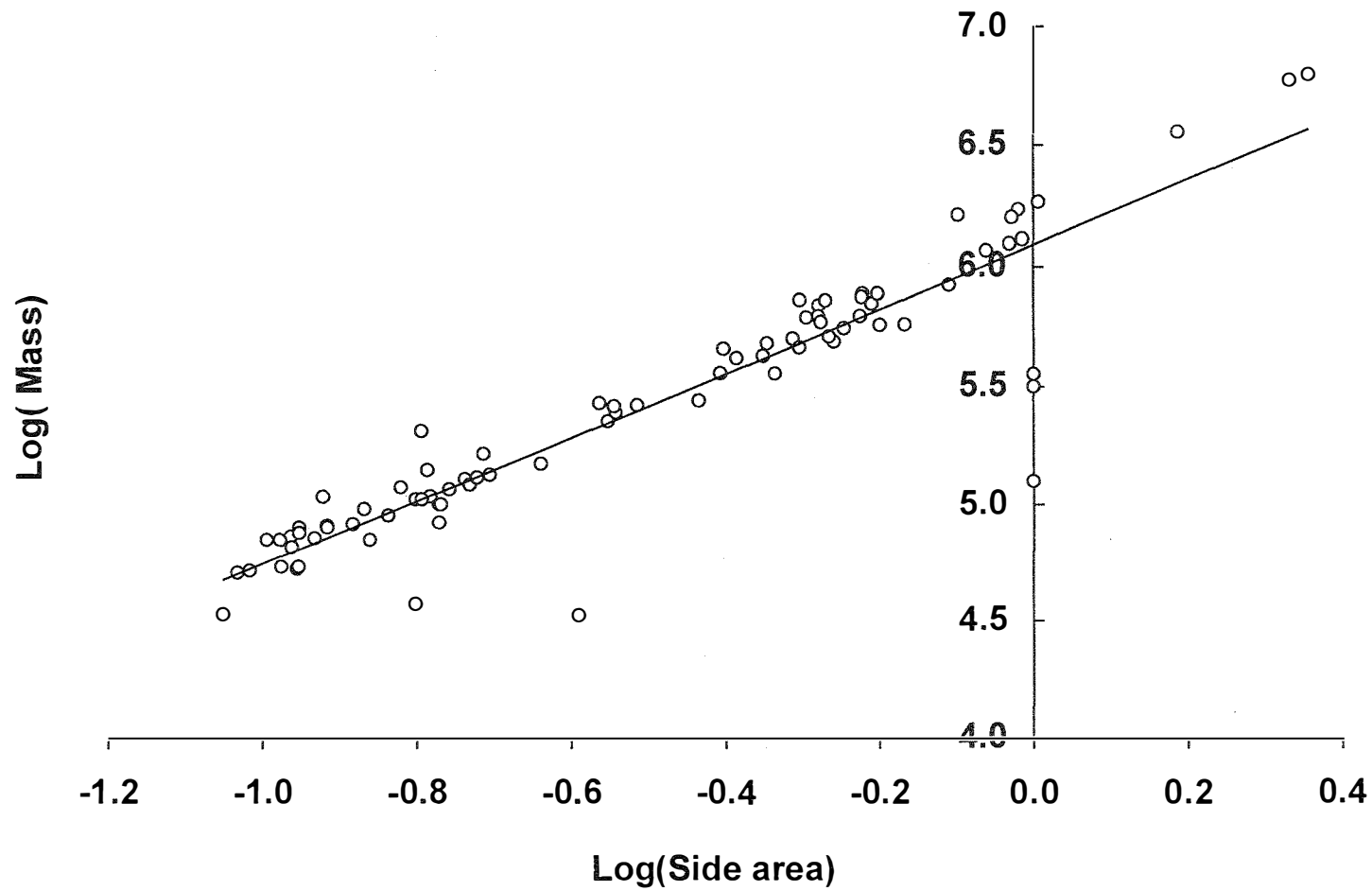


Figure 2.3. The relationship between body mass and side area for model #4. $\text{Log}_e M = 6.176 + 1.454(\text{Log}_e SA)$; $r^2 = 0.939$; 95% confidence interval ± 6.36 .

2.3.2 Post-lactation cows.

The most reliable model for cows contained morphometric and photographic variables (model 26, Table 2.3). However, the 95% confidence interval was only increased by 0.56% when morphometric variables alone were used (model 21, Table 2.3). Overall, this animal class produced the best 95% confidence interval for all models, $\pm 2.66\%$ (model 26, Table 2.3). Models specific to the cow subgroup were generally better predictors of body mass than models containing the same variables, derived from the total pool.

2.3.3 Yearlings.

Of all yearling models, the most reliable contained both variable types and had a confidence interval of $\pm 5.92\%$ (model 41, Table 2.4). Models obtained for this class were the least reliable in terms of confidence intervals.

2.3.4 Comparison of morphological characteristics and photographic measurements.

Using a Student *t*-test, it was shown that the physically measured axillary girth (G) was not significantly different ($t_{55} = -1.520$, $n = 56$, $P = 0.134$) to the equivalent photographic variable GP. As expected, STL was significantly different ($t_{84} = 5.616$, $n = 85$, $P < 0.001$) to photographically measured L as these measurements were taken from different locations at the subjects' caudal end.

2.4 Discussion.

Body masses of pinnipeds were estimated with a high degree of certainty using both morphometrics and photogrammetry, however the best model in this study contained only the morphometric parameters STL and G. Accuracy was marginally improved when class-specific models were used for cows but not yearlings.

Presumably, this is related to intersex differences in body composition (see Haley *et al.* 1991) and growth pattern (Bryden 1968a), and age-dependent growth rate (Bryden 1968a). Further, when using class-specific test cases for the general models (Table 2.2), the confidence intervals were, in general, minimally increased for both yearlings and cows when compared to those of specific models (Tables 2.3 and 2.4). Increased sample size and variation in body condition may be accounted for in the general models (Table 2.2), and may explain this finding. In developing models for yearlings, data for males and females were combined as sexual dimorphism is not apparent in this age class (Chapter 3).

2.4.1 Photographic variables only.

Although models which included only photographic variables were the least reliable, they still produced relatively high confidence intervals. Much of the variation unaccounted for by these models is possibly related to the digitising and tracing procedure. Accuracy of tracing images with a digitiser depended on the quality of the images and also the skill of the operator. Four tracings were undertaken for each image in an attempt to account for such variations. Haley *et al.* (1991) repeated tracings of each image so that measurements were consistently within 1 to 2% of each other. A similar consistency was achieved in this study. The

position of the animal whilst photographing was critical in terms of quality of the digital tracings. Animals needed to be on a firm and packed down surface such as sand rather than long grass or beach shingles so that, particularly, an exact ventral outline could be distinguished.

Haley *et al.* (1991) found that STL was approximately 10% longer than L, whilst this study found it to be only 3%. This difference was possibly related to the operator's selection of the 'base of the hind flippers'. The measurements of girth and GP were not significantly different, which verified the relative accuracy of estimation of linear measurements by way of photogrammetry in this study. Side area was found to be the best correlated single variable, a finding made also by Haley *et al.* (1991) and Modig (1995). A likely reason for this is that side area is influenced by both length and girth (Haley *et al.* 1991).

2.4.2 Morphometric variables only.

The best predictor of body mass was a combination of the morphometric variables body length and girth squared. This corresponds to previous studies of Steller sea lions (*Eumetopias jubatus*), Weddell seals (*Leptonychotes weddellii*), walruses (*Odobenus rosmarus*) and southern elephant seals that have used this combination (body volume index) as a reliable predictor of body mass (Gales and Burton 1987; Castellini and Kooyman 1990; Castellini and Calkins 1993; Knutsen and Born 1994). This is a practical model to use in field situations, as these variables are easily measured in a sedated animal.

Body composition is an important consideration when deciding whether to utilise general or class-specific models for the body volume index. For example, Woods (1994) observed considerably less variation in condition (*i.e.* blubber levels) of cows at the end of lactation, compared with the beginning of the breeding season. Because of this, post-lactation cow mass was possibly better predicted by the class-specific model (model 21, Table 2.3) than the general model. Conversely, the yearlings in this study appeared to vary considerably more in body condition (C. Bell, *pers. obs.*) and consequently, the general model (model 6, Table 2.2) was more reliable than the equivalent yearling-specific model. There was also a bias towards the yearling age group in the total sample used for the regressions. Another explanation for this difference between yearlings and cows is the greater relative error involved with making morphometric measurements of small animals (yearlings) compared to large animals (cows and bulls).

Interestingly, models derived in this study with the single calculated variable of body volume (*unpub. data*) were considerably less reliable than those which contained length and girth squared. Although the truncated cones method has been validated to give realistic blubber mass values (Slip *et al.* 1992b), estimation of absolute body volume has not. Accuracy may have been reduced as this model did not account for differences in body composition between the different age classes or the different densities of adipose and lean tissue.

It must be emphasised that repeat morphometric measurements can vary considerably for one individual. Repeated STL measurements of northern elephant

seal bulls may result in an error of between 2 (Haley *et al.* 1991) and 3% (Clinton 1994). Higher variations such as 4% have been noted in southern elephant seal cows (C. Bell, *unpub. data*). This variation greatly depends on the surface that the seal is lying on and the positioning of the neck, and this must be taken into consideration when making such field measurements.

2.4.3 Photographic and morphometric variables combined.

The best cow and yearling models, in terms of mass predictability, contained both types of variables. But for both subgroups, only marginal improvements in confidence intervals were made when using the combined variables over morphometric variables alone (Tables 2.3 and 2.4). This improvement would not warrant the extra labour involved with obtaining photographs and processing them.

2.4.4 Comparison with other studies.

In comparison to photogrammetry studies of northern elephant seal bulls (Haley *et al.* 1991) and southern elephant seal cows (Modig 1995), the r^2 values obtained in this study were considerably higher (Table 2.5). When post-partum cow models from this study were compared with Modig (1995) however, r^2 values were very similar. Haley *et al.* (1991) calculated confidence intervals using the measurements included in the models, however these could not be compared as the present study used test cases which were not used in the derivation of models. Thus, a direct comparison could not be made on this basis, however r^2 values in this case are adequate indicators as they at least quantify the degree of variation in body mass attributable

Table 2.5. Comparison of r^2 values for power models for the present study (utilising all ages and classes), Haley *et al.* (1991) and Modig (1995).

	Haley <i>et al.</i> (1991)		Modig (1995)		Present study	
Age class	Bulls only		Cows only		Yearlings, cows and immature males	
Variable	r^2	n	r^2	n	r^2	n
GA	0.765	71	-	-	0.950	48
L	0.778	85	0.682	39	0.894	80
SA	0.923	84	0.840	39	0.973	80
L, GA	0.897	71	-	-	0.980	45
L, SA	0.928	84	-	-	0.973	80
SA, GA	0.940	70	-	-	0.983	45
SA, GA, L	0.948	70	-	-	0.984	45
H3	-	-	0.649	39	0.884	71

to the dependence of mass on the included variables (Modig 1995). In general, a higher degree of variation was accounted for in this study. Other differences between these studies are likely to relate to the different age classes used, seasonal changes in body condition and image analysis techniques utilised. In this connection, it can be noted that the visual selection of ‘the base of the hind flippers’ is an important factor in determining SA, the most powerful of the photographically estimated variables. Modig (1995) noted a significant improvement in results when a projection method for image analysis was used instead. This warrants further assessment and could potentially increase the accuracy of such a technique developed here, although the advantage with digital imagery is the relative speed and ease with which processing is undertaken.

2.4.5 Recommendations.

With sedation of specimens, it is preferable to directly measure snout-tail length and girth (*e.g.* model 21, Table 2.3 and model 36, Table 2.4) rather than use photogrammetry for indirect mass estimation of southern elephant seals. This would be useful particularly when subjects were amongst rocks or high grass and unsuitable for photographing, for example when retrieving electronic dive recorders. For studies focused on a particular class of animal, it is recommended to develop models specific to that group, to account for body size and seasonal fluctuations in body condition.

Photogrammetry may have a role when animals are motionless, lying on a flat substrate and sedation is not necessary, although this depends on how fractious and

approachable the subjects are. Of all classes of elephant seal, this may only be applicable to bulls as they are generally approachable without disturbing whilst in a non-sedated state. Irrespective of age class, the most useful model (model 4, Table 2.2) for photogrammetric mass estimation includes the single variable side area, *i.e.* $\text{Log}_e M = 6.176 + 1.454(\text{Log}_e SA)$. Minimal labour is needed to obtain the single side photograph for this measurement. With addition of girth area (model 1, Table 2.2; $M = 849.288(GA^{0.462})(SA^{1.071})$), confidence intervals are improved, however obtaining the second photograph would be difficult in a non-sedated seal. A useful application would be, for example, the estimation of the biomass of adult elephant seal bulls at a breeding site. A large number of mass estimations could be rapidly generated without manually weighing or making morphometric measurements. However, technical equipment required is often not available in field situations, limiting the rapidity of obtaining results.

The ultimate decision between the use of morphometric or photographic variables would depend on the size and location of animals, accuracy of mass determination required and time available. For studies requiring large numbers of body masses in a short time frame, photogrammetry would be a relatively reliable method of mass estimation. Where weighing equipment cannot be transported and animals must be sedated, morphometric variables are best suited for indirect mass estimation. Studies, however, requiring exact individual body mass measurements, energetics studies for example, would continue to be best undertaken by weighing animals using standard equipment such as tripods and scales.

2.5 Summary.

A simple, photographic technique was developed to indirectly estimate body mass for southern elephant seal cows (post-lactation), yearlings, and immature males and females. Regressions of mass on both photographic and morphometric variables (together and separately) yielded useful, predictable models. Using such variables, the best estimation of the actual mass was for post-lactation cows, with a 95% confidence interval of $\pm 2.66\%$ of the predicted body mass. Although combining photographic and morphometric variables produced the most reliable models specifically for cows and yearlings, the most practical model contained only the morphometric variables length and girth squared. Side area was the best correlated single photographic variable and this corresponded with other studies.

Photogrammetry could be useful when animals cannot be sedated and are located on a flat surface, but does require animals to be motionless when approached. Thus, the procedure may be more suited to bulls rather than other age classes, and could have a role in studies where large numbers of mass estimations are rapidly required. If sedation is utilised in smaller animals, then the use of body length and girth is the most suitable, indirect mass estimation technique to overcome the use of heavy weighing equipment.

CHAPTER THREE

GROWTH DURING THE FIRST FORAGING TRIP.

3.1 Introduction.

Growth of juvenile mammals can have implications for numerous life history attributes manifested both in juvenile and adult life. Most obviously, juvenile growth may determine size later in life (Gosling and Petrie 1981; Suttie and Hamilton 1983; Festa-Bianchet *et al.* 1996). Ultimately, adult body size can affect reproductive success (Clutton-Brock *et al.* 1982). Juvenile mortality is also influenced by juvenile growth (Clutton-Brock *et al.* 1982; Promislow and Harvey 1990), which may indirectly be influenced by population density and food resources (Skogland 1985; Solberg and Saether 1994)

Like other mammals, the first year of life is a critical growth period for phocid seals, as pups must grow rapidly during a short period of maternal care to obtain adequate body reserves of blubber for thermoregulation (Bryden 1969c), and the ensuing post-weaning fast (Worthy and Lavigne 1983). Phocid pups are precocious, their large birth size and fast growth being advantageous in providing thermal benefits (Kovacs and Lavigne 1986; Worthy 1987) and supposed survival benefits whilst at sea. Once pups have survived the protracted post-weaning fast, they must then undergo the transition from terrestrial fasting to aquatic foraging, contending with several obstacles. There is a necessity to rapidly gain swimming skills and develop physiological mechanisms to enable efficient diving and foraging (Arnbom

et al. 1993; Thorson and Le Boeuf 1994). Adequate blubber must be available as an energy source for this transition period (Worthy and Lavigne 1983).

Numerous studies have characterised the preweaning growth phase of the southern elephant seal (*e.g.* Laws 1953; Bryden 1968b; Little *et al.* 1987; Hindell *et al.* 1994c). By contrast, there has been no comprehensive study of growth in the subsequent months of the first year of life, nor has there been for other phocids. Hindell and Burton (1987) emphasised the need for investigating this important component of the life history during which high mortalities are recorded (Carrick and Ingham 1962b; Hindell 1991). Further, foraging behaviour, feeding grounds and prey species consumed may fundamentally differ between this age group and adults (Hindell *et al.* 1994b), which have been more widely studied. Although adult male and female southern elephant seals from Macquarie Island exploit different foraging areas (Hindell *et al.* 1991b), little is presently known about the movements or diet of juveniles from any southern elephant seal population. Only recently have preliminary details of diet and foraging behaviour of juveniles been elucidated (Green and Burton 1993; Slip 1995; Slip *in press*). If juvenile males and females are targeting different prey species and utilising different feeding grounds and foraging techniques, then sex differences in first year growth rate may be expected. Further, differences in diving ability may be linked to body size, with larger body size conferring greater oxygen stores (Kooyman *et al.* 1983) and lower mass-specific metabolic rate (Costa 1993). If differences such as these exist, then the extreme sexual dimorphism of adult southern elephant seals (Ling and Bryden 1981) is predicted to become apparent during this time.

Similarly, northern elephant seals experience high mortalities during the first foraging trip (Reiter *et al.* 1978; Le Boeuf *et al.* 1996). Current evidence suggests that first trip animals migrate in the general direction of older juveniles and adults (Le Boeuf *et al.* 1996; Condit and Le Boeuf 1984), and have similar dive patterns (Thorson and Le Boeuf 1994; Le Boeuf *et al.* 1996), but are operating under physiological limitations (Le Boeuf *et al.* 1996). Limited data is available for first trip diet of northern elephant seals (*e.g.* Condit and Le Boeuf 1984; Hacker Sinclair 1994).

Southern elephant seal pups are born between September and November in harems of varying sizes (Ling and Bryden 1981). Although blubber increases from 3% of body weight at birth to approximately 40% at weaning, lean tissue remains at constant level until the last few days of lactation when it rapidly increases (Hindell *et al.* 1994c). Weaned at approximately 23 days, pups then undergo a post-weaning fast (Carrick *et al.* 1962a). Pups depart at approximately 10 weeks of age (Ling and Bryden 1981), having lost approximately 30% of their weaning mass during the fast (Wilkinson and Bester 1990; Arnborn *et al.* 1993), and then haul-out intermittently during the following months after the first foraging trip (Hindell and Burton 1988a). Such a life history, combined with a high philopatry (Nicholls 1970), allow for early-life longitudinal growth studies to be undertaken in conjunction with intensive mark-recapture programs.

The aim was to (i) characterise juvenile growth of southern elephant seals of the Macquarie Island population during their first foraging trip; (ii) discern factors that

lead to proportionally greater body size at 12 months of age; (iii) infer differences in foraging behaviour between males and females; and (iv) compare this growth pattern to northern elephant seals.

3.2 Methods.

Field work was undertaken at the isthmus study area (Carrick *et al.* 1962a) of Macquarie Island between March and November, 1994. Daily surveys of the isthmus were conducted to identify animals that had hauled-out within the previous 24 hours, after returning from their first foraging trip. These animals were individually marked by flipper tags and hot-iron brands during the 1993 pupping season, and had been weighed at birth and weaning (McMahon *et al. in press*). Timing of birth and weaning had been determined by daily observations of breeding females (McMahon *et al. in press*). Snout-tail length was not recorded for these pups at that time. As this study was commenced after departure of weaners, departure date was estimated by adding 45 days to the known weaning date (Arnbom *et al.* 1993). Departure mass was calculated by taking 68% of the weaning mass (Wilkinson and Bester 1990; Arnbom *et al.* 1993). Estimated departure mass was used in analyses instead of weaning mass to account for mass-loss during the post-weaning fast.

Seals returning to the isthmus were physically restrained with a canvas head bag and sedated by intravenous injection of approximately 0.9 mg/kg of ketamine and 0.03 mg/kg of diazepam, using an 18 g, 90 mm spinal needle (see Slip and Woods 1996).

Mass (defined as return mass) was obtained to the nearest kilogram, by suspending the seal in a stretcher from an aluminium tripod using an electronic strain-gauge of 2500 kg capacity (± 1 kg accuracy). Snout-tail length (straight line) was measured with the animal in ventral recumbency with a glass fibre tape-measure. Repeat measurements of individuals at subsequent haul-outs were not undertaken. A census of the isthmus for juvenile southern elephant seals (visually defined as having a snout-tail length less than 2.0 m) was also undertaken on alternate days between March and September 1994.

Growth of 41 males and 32 females, between 5 and 12 months of age, was described by changes in snout-tail length, return mass, daily growth rate (estimated between departure and first haul-out), condition index (CI; mass/ snout-tail length) and performance index (PI; return mass/birth mass). Where applicable, growth variables were transformed into natural logarithms and analysed using linear regression models. Age throughout the study was measured in months. Sex differences in regression slopes and intercepts were examined using analyses of covariance (ANCOVA). A Student-*t* test was used to test for significant differences between means. Significance for all statistical tests was assumed to be at the $P < 0.05$ level. Values are presented as mean \pm standard deviation, unless otherwise stated.

3.3 Results.

3.3.1 Growth and time at sea.

A significant positive relationship was demonstrated for return mass with time for both sexes between 5 and 12 months of age (Figure 3.1). There was no difference between the sexes in the return mass and age relationship (slope ANCOVA: $F_{1,69} = 0.53$, $P > 0.05$; intercept ANCOVA: $F_{1,70} = 1.24$, $P > 0.05$), although there was considerable age-specific variation in body mass within the sexes. A significant increase in snout-tail length (STL) with return age was recorded ($\text{Log}_e\text{STL} = 0.29\text{Log}_e\text{Age} + 0.11$, $r^2 = 0.10$, $F_{1,60} = 7.86$, $P = 0.007$). Return mass (M_R) was positively correlated with snout-tail length ($\text{Log}_eM_R = 2.58\text{Log}_e\text{STL} + 3.57$, $r^2 = 0.72$, $F_{1,60} = 156.68$, $P < 0.001$), and there was no significant sex difference for this relationship (slope ANCOVA: $F_{1,58} = 0.10$, $P > 0.05$; intercept ANCOVA: $F_{1,59} = 0.08$, $P > 0.05$). Using the above models, subjects between 5 and 12 months of age were estimated to increase their snout-tail length by approximately 10% and body mass by 45%. A positive increase in condition (CI) and performance (PI) indices with age was noted during the first foraging trip ($\text{Log}_e\text{CI} = 0.09\text{Log}_e\text{Age} + 0.28$, $r^2 = 0.14$, $F_{1,60} = 10.78$, $P = 0.002$; $\text{Log}_e\text{PI} = 0.27\text{Log}_e\text{Age} + 0.68$, $r^2 = 0.10$, $F_{1,66} = 8.22$, $P = 0.006$).

Figure 3.2 illustrates the overall change in body mass during the first year of life. Return mass did not exceed weaning mass until 7 months of age ($F_{10,258} = 104.44$, $P < 0.001$; Tukey test $P = 0.005$). As expected, rapid mass changes, both positive and negative, occur in the first 2.5 months of life, followed by a steady increase in mass over the next 9.5 months, ultimately doubling the departure mass at 12 months of

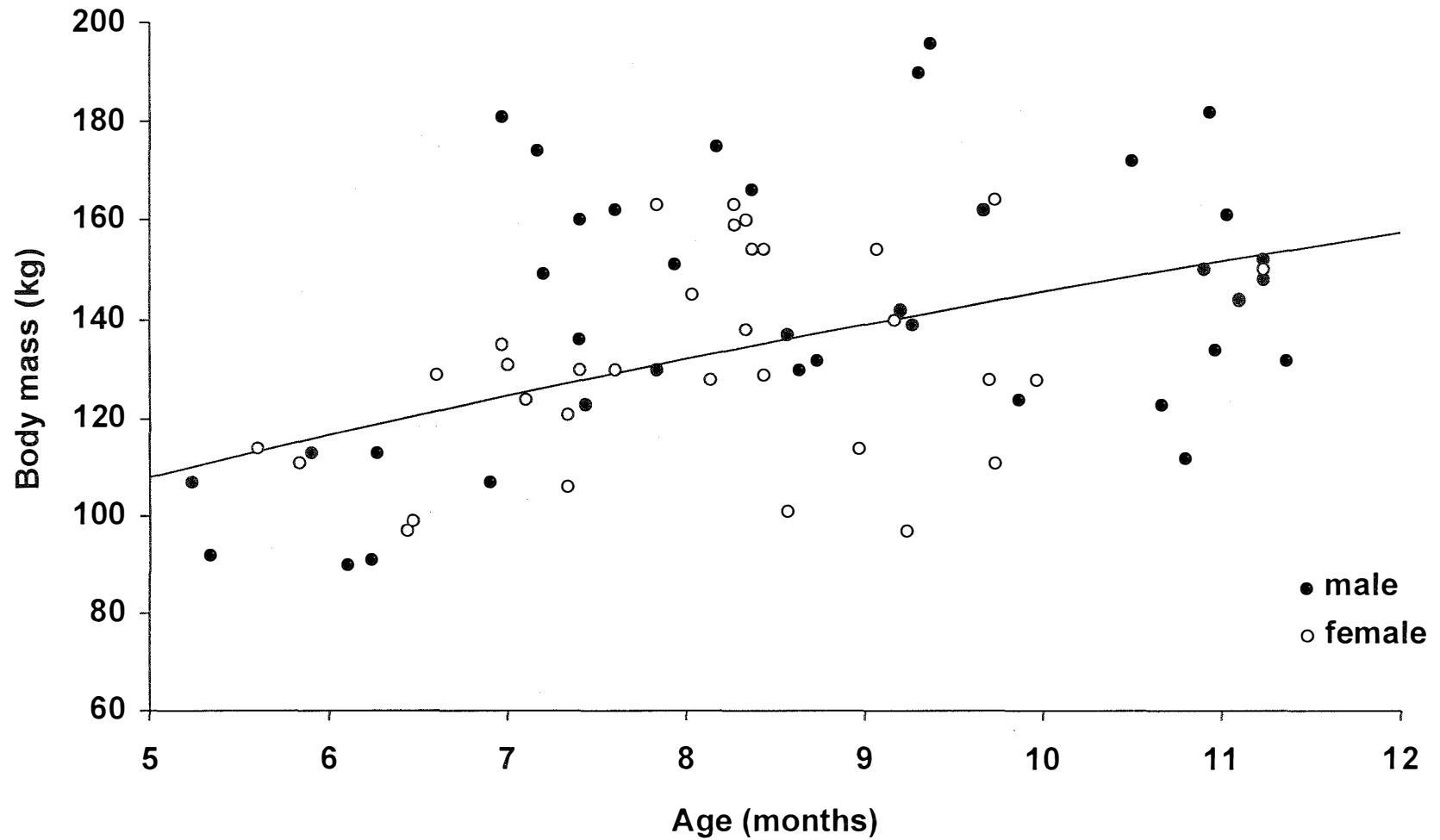


Figure 3.1. Logistic curve fitted to illustrate the relationship between return mass (M_R) and age at haul-out after the first foraging trip for both sexes. $\text{Loge}M_R = 0.43\text{LogeAge} + 3.99$; $r^2 = 0.23$; $F_{1,71} = 21.96$; $P < 0.001$.

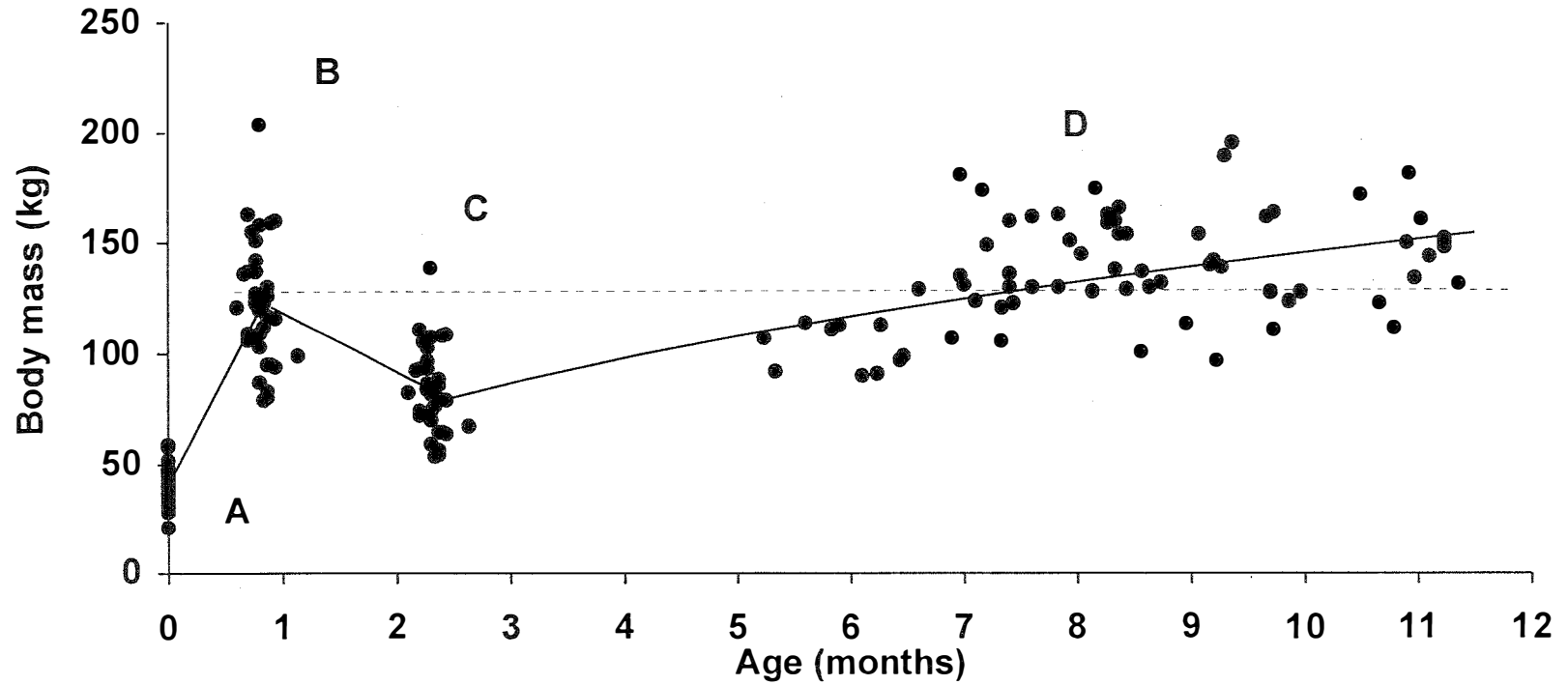


Figure 3.2. Change in body mass (M) during the first 12 months of life for males and females. The dashed line represents the mean weaning mass (123 ± 27 kg, $n = 36$). The groups of animals are: A, at birth; B, at weaning; C, at departure; and D, at return after the first foraging trip. Data points of the C group were estimated; all other points were measured.

Birth to weaning (A to B): $M = 98.45\text{Age} + 40.72$; $r^2 = 0.81$; $F_{1,100} = 422.52$; $P < 0.001$.

Weaning to departure (B to C): $M = -26.80\text{Age} + 145.21$; $r^2 = 0.44$; $F_{1,70} = 57.20$; $P < 0.001$.

Departure to return (C to D): $\text{Loge}M = 0.43\text{LogeAge} + 3.99$; $r^2 = 0.23$; $F_{1,71} = 21.96$; $P < 0.001$.

age. The age-specific variation observed in the first 2 months of life appeared to be maintained throughout the first year of life.

There was no significant relationship between birth mass and subsequent growth rate (ANOVA, $F_{1,62} = 0.70$, $P > 0.05$). Although growth rate to 12 months of age was not significantly related to departure mass (ANOVA, $F_{1,62} = 3.28$, $P > 0.05$), when the sexes were examined separately, growth rate was found to be negatively related for females (Figure 3.3), but not males (ANOVA, $F_{1,34} = 0.29$, $P > 0.05$). A female departing at 110 kg, for example, would be expected to grow at 0.25 kg/day, whilst a 50 kg departure mass would have a subsequent growth rate of 0.43 kg/day.

A mean period of 182 ± 51 days ($n = 64$) were spent at sea by both sexes (Figure 3.4), with no significant sex difference ($t_{62} = 1.27$, $P > 0.05$). Subjects had a mean growth rate of 0.34 ± 0.12 kg/day ($n = 64$) during this period, with no significant sex difference ($t_{62} = -0.88$, $P > 0.05$). Subjects gained 57.5 ± 16.4 kg ($n = 67$), or 75.4 ± 26.6 % ($n = 67$) of their departure mass, during the first foraging trip. No sex difference was recorded for absolute or percentage mass-gain (respectively, $t_{65} = -0.03$, $P > 0.05$; $t_{65} = -1.73$, $P > 0.05$).

Duration of the foraging trip was positively correlated with return mass ($r^2 = 0.14$, $F_{1,62} = 11.11$, $P = 0.001$) and estimated departure mass ($r^2 = 0.10$, $F_{1,62} = 7.92$, $P = 0.007$). Birth mass did not affect time spent at sea ($F_{1,62} = 2.25$, $P > 0.05$). A negative relationship was found between daily growth rate (GR) and days at sea (T_S)

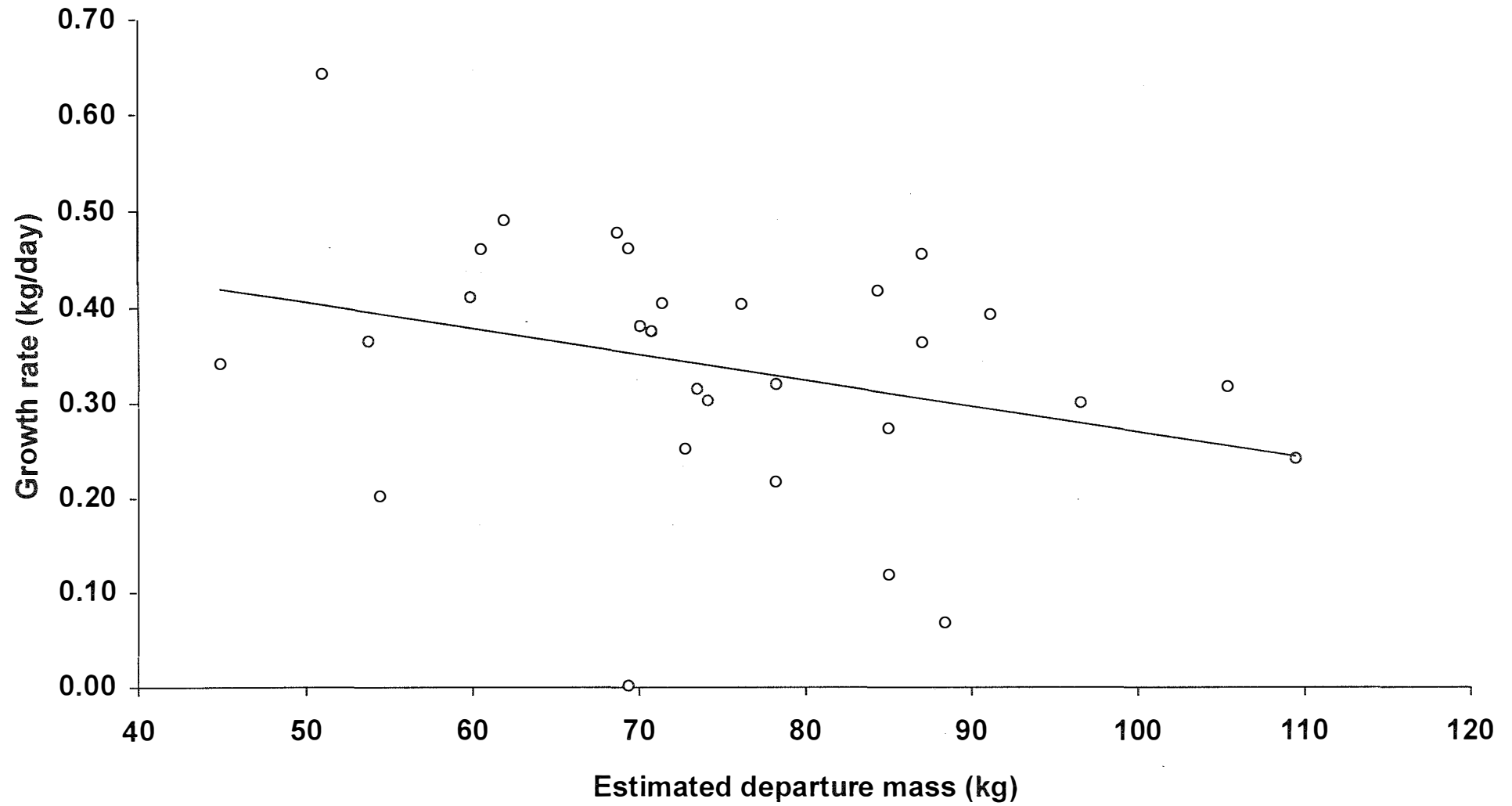


Figure 3.3. Linear relationship of mean daily growth rate (GR) and estimated departure mass (M_D) for female animals only.

$GR = -0.003M_D + 0.58; r^2 = 0.16, F_{1,26} = 4.98; P = 0.035.$

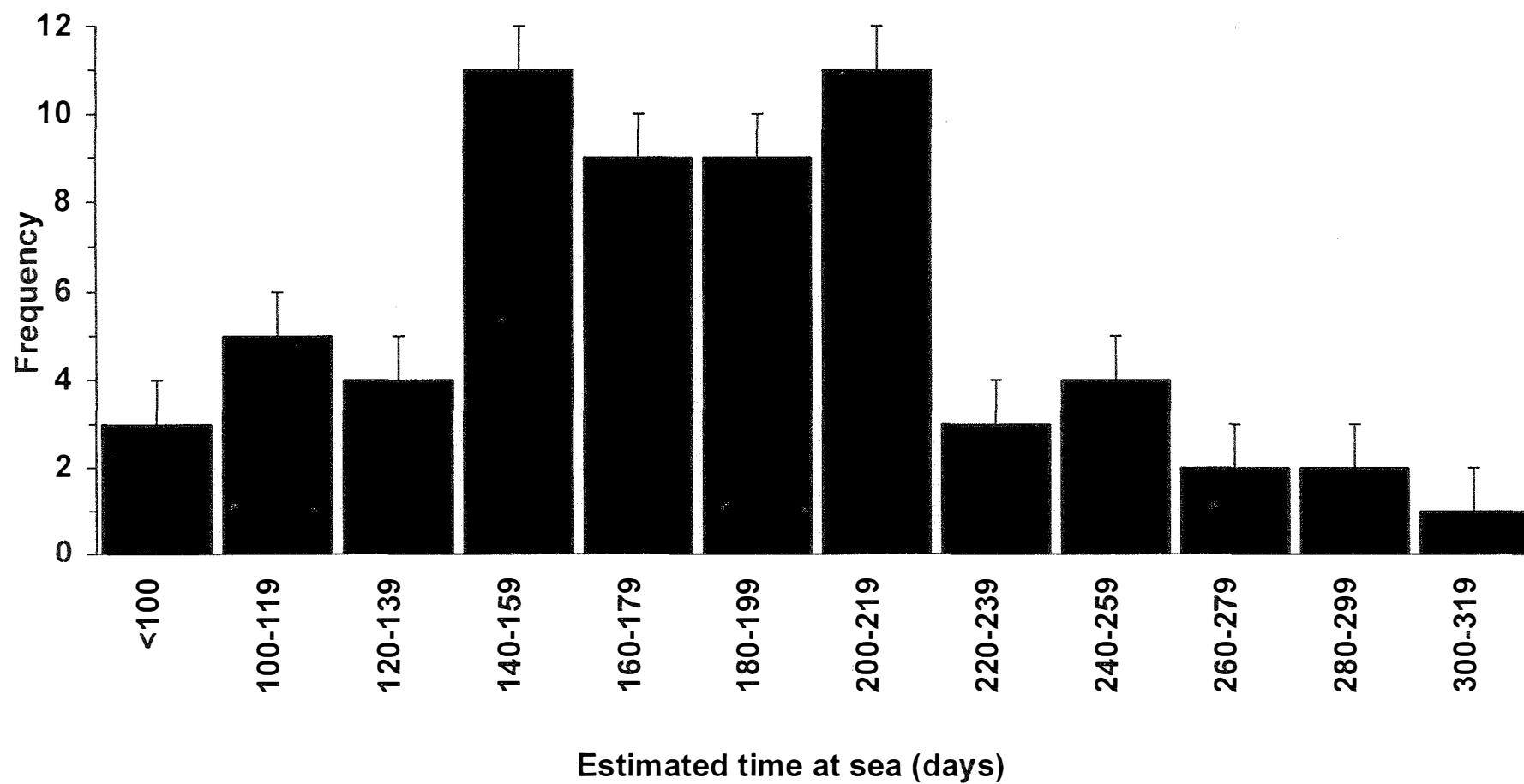


Figure 3.4. Histogram showing estimated duration of the first foraging trip, with standard error bars.

($GR = -0.001T_S + 0.57$, $r^2 = 0.30$, $F_{1,62} = 28.19$, $P < 0.001$), with a difference of 100 days at sea estimated to produce a difference of 0.1 kg/day.

3.3.2 Effect of birth and departure mass.

Return mass (M_R) was positively related to both birth mass (M_B) and estimated departure mass (M_D) ($\text{Log}_e M_R = 0.66\text{Log}_e M_B + 2.49$, $r^2 = 0.36$, $F_{1,66} = 38.56$, $P < 0.001$; $\text{Log}_e M_R = 0.62\text{Log}_e M_D + 2.20$, $r^2 = 0.55$, $F_{1,65} = 82.14$, $P < 0.001$), and again, there was no significant sex difference for the two relationships (M_B : slope ANCOVA, $F_{1,64} = 2.27$, $P > 0.05$; intercept ANCOVA, $F_{1,54} = 0.51$, $P > 0.05$. M_D : slope ANCOVA, $F_{1,63} = 3.91$, $P > 0.05$; intercept ANCOVA, $F_{1,53} = 0.42$, $P > 0.05$). Departure mass ($r^2 = 0.55$) accounted for more variation in return mass than birth mass ($r^2 = 0.38$).

3.3.3 Haul-out pattern.

The peak number ($n = 318$) of juveniles during the study period occurred on the 18th of May, 1994. The performance and condition indices were significantly lower for subjects hauled out 2 to 4 months post-departure (early; austral autumn), than 5 to 7 months (mid; austral winter) or 8 to 11 months post departure (late; austral spring), with no significant difference between mid and late haul-out animals (Table 3.1). This indicates that subjects were gaining relatively less mass during the early part of the first trip, despite having a higher daily growth rate. A similar seasonal difference was noted for absolute return mass (Table 3.1).

Table 3.1. Comparison of growth parameters for animals returning early (2-4 months post-departure); mid (5-7 months post-departure) or late (8-11 months post-departure) from their first foraging trip.

Variable	ANOVA	r^2	Probability	Tukey test for comparison between return periods		
				Early and mid	Early and late	Mid and late
Return mass (kg)	$F_{2,70} = 11.44$	0.25	<0.001	<0.001	<0.004	ns
Performance index	$F_{2,63} = 27.77$	0.44	<0.001	<0.001	<0.001	ns
Condition index	$F_{2,53} = 9.28$	0.26	<0.001	<0.001	<0.001	ns

ns = not significant

3.4 Discussion.

The first year of life is a difficult time for juvenile elephant seals (Hindell and Burton 1987; Le Boeuf *et al.* 1994), especially during the pelagic phase when, without maternal guidance, they have to travel long distances and forage (Le Boeuf *et al.* 1996; Slip *in press*), as well as avoid predators (Le Boeuf and Laws 1994). It has been shown for harp seals (*Phoca groenlandica*) and grey seals (*Halichoerus grypus*) that a large proportion of energy intake during this period may be devoted solely to thermoregulation (Worthy 1987). Relatively more energy would be expected to be expended for thermoregulation in under-sized animals, resulting in less energy being available for somatic growth and blubber deposition. Further, because juveniles undergo somatic growth, they need to gain relatively more mass than adults, despite the higher mass-specific locomotory costs for proportionally smaller body size (Boyd *et al.* 1994a). For example, animals were found to increase their body mass by 75% during the first foraging trip in this study, whilst mature cows may increase their body mass by only c.36 % (blubber deposition) during the post-moult period (Hindell *et al.* 1994a; Hindell and Slip *in press*).

Most juvenile mortality to one year of age in elephant seals occurs whilst at sea (Hindell 1991; Le Boeuf *et al.* 1994). For southern elephant seals, 40 to 60% die during the first year foraging trips (McCann 1985; Hindell 1991; Bester and Wilkinson 1994). A similar mortality has been recorded for northern elephant seals (Reiter *et al.* 1978; Le Boeuf *et al.* 1994). Such mortality rates suggest the transition to pelagic life is an arduous process (Le Boeuf *et al.* 1994; Le Boeuf *et al.* 1996),

thus demanding a rapid, energy efficient transition to pelagic life, to enable survival, foraging success and concomitant growth.

3.4.1 Growth and body composition.

Southern elephant seals, that survive their first foraging trip, increase in both body length and mass, but undergo a relatively larger mass increase. This is consistent with Laws (1953), who described the pattern of first year growth as the consolidation of skeletal structures and the strengthening of muscles, and conforms with the observation that yearlings are of sleeker appearance than weaners (C. Bell, *pers. obs.*). Although growth of adipose tissue, followed by bone, peaks before departure, muscle growth attains its maximum rate whilst at sea (Bryden 1969c). This means there is a differential tissue growth order of fat, bone, then muscle. In contrast, terrestrial mammals have a differential growth pattern order of bone, muscle, then fat (Pålsson 1955). For example, skeletal growth of red deer (*Cervus elaphus*) continues over the feed-restricted winter months, despite little growth of other body components (Mitchell *et al.* 1976). For elephant seals, the pattern of growth may be related to the priority of rapidly developing fat reserves to survive the post-weaning fast. Maximum growth of muscles, rather than bone, may then occur after departure as a result of the functional demands of aquatic life, rather than an urgent need to increase gross body size (*i.e.* by skeletal growth). For example, the epaxial muscles necessary for aquatic locomotion, undergo rapid growth during the pelagic phase (Bryden 1969c). Hence, the larger estimated percentage increase in body mass than body length (equivalent to skeletal size).

Increased muscle mass is also critical for optimising body oxygen stores, allowing for increased aerobic dive limits (Kooyman *et al.* 1983).

Instead of having rapid skeletal growth, the skeleton may instead undergo remodelling and strengthening, without any major change in overall dimensions. Skeletal growth may be limited further during the first pelagic phase because of other stressors acting concurrently. For example, severe nutritional restrictions during the first winter period of juvenile red deer (Mitchell *et al.* 1976; Suttie and Hamilton 1983) and reindeer (*Rangifer tarandus tarandus*) (Reimers 1972), may affect skeletal growth. If prey were limited for this elephant seal age class, then body length increase may be minimal because of the nutritional restrictions placed on skeletal growth. It would be expected however, that blubber would be at least maintained at the expense of skeletal growth, for thermoregulation and basal metabolism. Interannual variations in subyearling growth, yet to be studied, may also reflect annual variations in energy content of prey species (Worthy 1987; Martensson *et al.* 1996).

3.4.2 Short-term effects of first year body size.

Body size at birth and departure plays an important role in determining body size during the first year. For northern elephant seals, mass at weaning accounts for 25% of the variation in mass at one year of age (Morris *et al.* 1989, cited in Campagna *et al.* 1992). In this study, departure mass accounted for more variation in return mass than birth mass, indicating that postnatal factors have more influence than prenatal growth and investment. Arnbom *et al.* (1993) found a positive relationship between

weaning mass and daily mass loss during the fast, as well as weaning mass and fast duration, and suggested that heavier weaners, although losing more mass, may depart with improved foraging skills. Further, Wilkinson and Bester (1990) noted that male weaners (*i.e.* greater weaning mass) may have improved foraging skills. Postnatal factors, apart from absolute body size obtained, may include the social (Reiter *et al.* 1978; Arnborn *et al.* 1993) and physiological changes (Thorson and Le Boeuf 1994) that elephant seals undergo during the post-weaning fast. Rate of development of diving physiology, strengthening of locomotory muscle groups and learnt skills necessary for developing foraging techniques are specific examples.

Body growth over the first year of life of large mammals may also be altered by factors such as population density that influence food stocks (Klein 1968; Choquenot 1991; Trites and Bigg 1992; Hindell *et al.* 1994b; Solberg and Saether 1994;). Hence, growth rate may be a useful indicator of foraging conditions experienced during the first foraging trip, as suggested for caribou (*Rangifer tarandus caribou*) (Crête *et al.* 1993). With the availability of larger data sets in the near future, it will be interesting to study possible links between seasonal fluctuations in juvenile growth and diet/foraging behaviour.

Unexpectedly, this study found that heavier females at departure grow slower whilst at sea, despite foraging for a longer period than lighter counterparts. No such relationship was found for males. Despite a lower growth rate, heavier departing females still returned heavier (*i.e.* return mass was directly related to departure mass). If this negative relationship with growth rate was related only to body size,

then a similar relationship would be expected for males. Only those light female weaners that rapidly become proficient foragers, presumably survive the first foraging trip, as they have very limited energy stores: as foraging ability improves, these animals must rely on food intake as a source of energy rather than the already dwindling body stores of adipose tissue. A lower percentage of body weight as adipose tissue may also stimulate appetite (Condit and Ortiz 1987). If so, then smaller departing females may be stimulated to actively seek more food. In combination with an improved food conversion ratio for this group (Worthy and Lavigne 1983), this may result in the observed higher growth rate of lighter females as they undergo catch-up growth (Mosier 1985). Despite the higher growth rate, the combined effects of shorter time spent at sea, growth-related increase in metabolic rate and increased rate of heat loss (Worthy 1987), may account for a smaller absolute body mass than heavier departers.

Heavier departing females, on the other hand, may rely for longer on oxidation of adipose tissue as a source of energy. Although supposedly more proficient at foraging, this group may have a reduced appetite (Condit and Ortiz 1987) and may actually require greater effort for diving due to the effect of positive buoyancy (Fedak *et al.* 1994; Thorson and Le Boeuf 1994) despite improved diving ability (Kooyman *et al.* 1983) and lower mass-specific metabolic rate (Costa 1993). Conversion of adipose tissue to lean tissue would at least maintain body weight of this group (Condit and Ortiz 1987), and any extra food acquired would allow for growth. The reduced appetite of this group may be a mechanism to prevent the negative effects of excessive mass gain, as observed in big horn sheep (*Ovis*

canadensis) (Festa-Bianchet *et al.* 1996) and Arctic foxes (*Alopex lagopus*) (Prestrud and Nilssen 1995). Such a negative effect in elephant seals may be increased positive buoyancy.

Such a relationship may not exist for males because their body composition may be relatively more uniform, whether heavy or light, with generally lower adipose levels than females. Male Antarctic fur seals (*Arctocephalus gazella*) for example, have proportionally lower lipid reserves at birth and weaning than females (Arnould *et al.* 1996). Although male and female northern elephant seals have been recorded as having similar body composition during nursing (Kretzmann *et al.* 1993), sex differences are yet to be studied in southern elephant seals.

3.4.3 Development of sexual dimorphism.

This study suggests that sexual dimorphism may develop in southern elephant seals after 12 months of age. Laws (1953) and Boyd *et al.* (1994a) also showed the sexes were of similar size (mass and length) at 1 year of age, but differed after that. Carrick *et al.* (1962a) found that up to 3 years of age, males were only “slightly greater” than females in length. Although gross dimensions may not differ between the sexes, body composition might, as previously suggested, which presents an interesting future study. This shows that sexual dimorphism does not originate from different growth rates in the first year, but rather, during other phases of growth.

In bighorn sheep, sex differences in body mass, necessary for the development of sexual dimorphism, are most important beyond 2 years of age, when changes in

social and foraging behaviour demand development of sexual dimorphism (Festa-Bianchet *et al.* 1996). Similarly in southern elephant seals, sexual dimorphism may not become apparent until males can match their genetic growth potential with suitable feeding grounds and/or adequate foraging skills to exploit such resources. Higher growth rates in the first year of life may be unsustainable by males simply because they have neither the skills nor strength to forage suitable prey effectively.

3.4.4 Haul-out pattern during the first year of life.

The pattern of haul-outs is consistent with Carrick *et al.* (1962b) and Hindell and Burton (1988a). The actual reasons for returning to land are yet to be fully determined, but have been suggested as relating to skeletal development, storms or illness (Carrick *et al.* 1962b; Wilkinson and Bester 1990), or may simply be a need for physical rest. Subjects in this study hauling-out during autumn, had performed much poorer (with respect to performance and condition indices) than those hauling-out later (*i.e.* winter and spring), suggesting they may not have been as successful foraging. That departure mass rather than birth mass is weakly correlated to time at sea indicates that the post-weaning shore period may be the critical period for determining time spent at sea, *i.e.* learnt behaviour of weaned pups may influence foraging success. Longer-term survival of such animals is yet to be analysed.

Chance may also play a role in determining the growth success of animals returning in autumn, with respect to locating food. Such animals may remain much closer to Macquarie Island, diving to depths of 100 to 200 metres (M. Hindell, *unpub. data*), competing with other species such as penguins and fur seals. In contrast, those hauling-out later in the first year (*i.e.* at sea longer) may have developed an adequate

degree of competence and strength, travelled further and hence, were more successful in regards to return mass.

3.4.5 Other determinants of growth.

Many other factors acting prior to the departure of juvenile elephant seals may affect growth during the first foraging trip. During the nursing period, pup growth is positively influenced by maternal body size (McCann 1985; Arnborn *et al.* 1994; Deutsch *et al.* 1994). However, congenital birth defects (Liepold 1980), transfer of passive immunity (Sams *et al.* 1996), parasitic disease (Banish and Gilmartin 1992), traumatic injuries sustained in the harem (Bryden 1968b; Le Boeuf and Briggs 1977) and pup behaviour (*e.g.* milk stealing; McCann 1982; Reiter *et al.* 1978) may modulate growth positively or negatively. The long-term requirement of this growth phase is to produce such a body composition that will allow for the successful transition from a terrestrial fast to pelagic foraging. This transition requires departing with sufficient blubber for thermoregulation and metabolism, optimum body size and composition for diving ability (Kooyman *et al.* 1983), as well as adequate foraging skills.

3.4.6 Interspecific comparison.

Although southern elephant seals increased their body mass during the first foraging trip, there is limited evidence that northern elephant seals from Año Nuevo only maintain their departure mass (Thorson and Le Boeuf 1994) (Figure 3.5), despite the two species being at sea for similar durations (Le Boeuf *et al.* 1996; this study). However, northern elephant seals appear to be at sea for less variable periods of

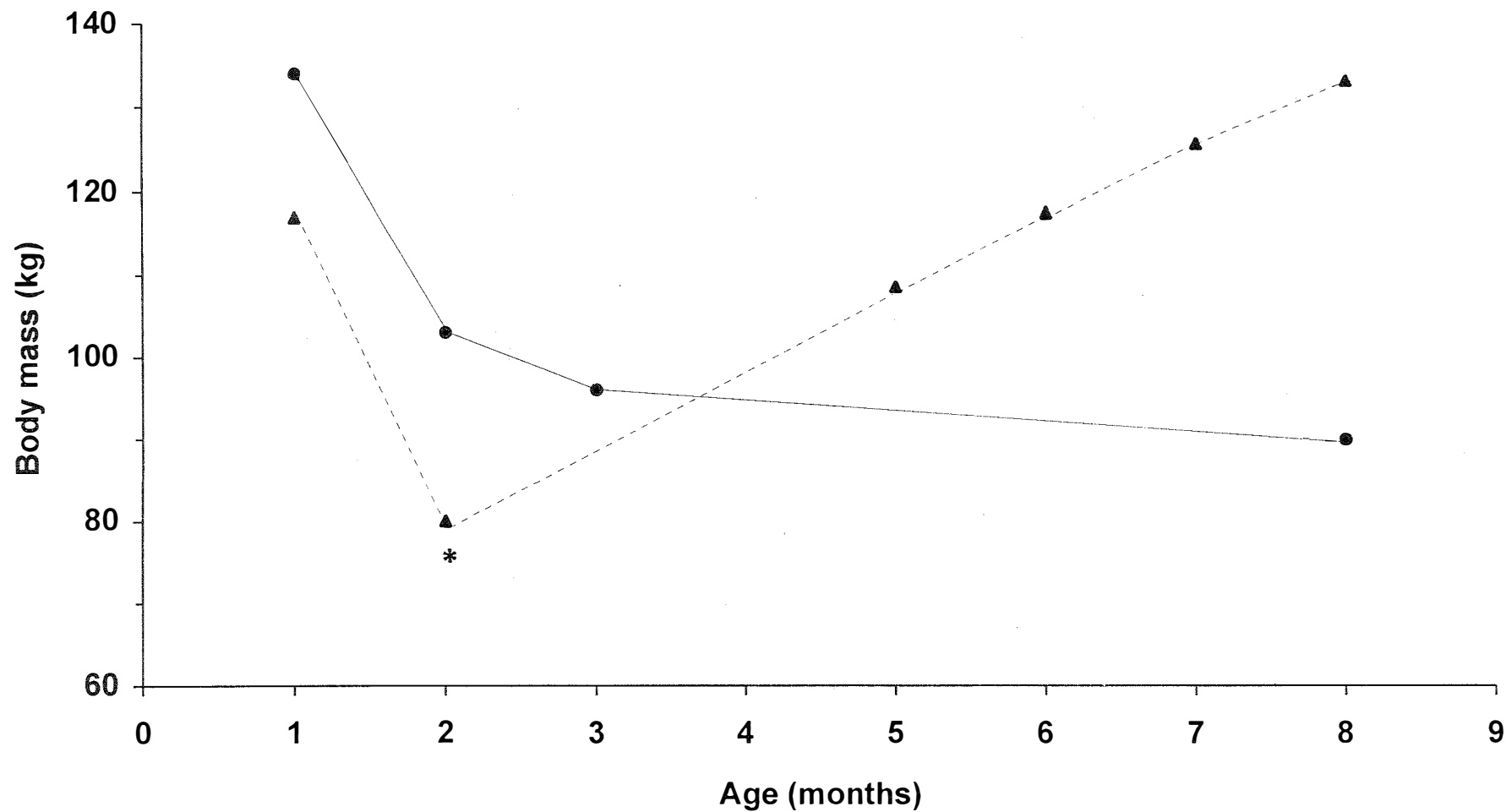


Figure 3.5. Comparison of growth of southern (broken line; this study) and northern elephant seals (unbroken line; Thorson and Le Boeuf 1994). Two month data point for *M. leonina* (*) was estimated; all other points measured.

time than southern elephant seals (Le Boeuf *et al.* 1996).

The accelerated growth of southern elephant seals may be due to a more predictable, reliable and possibly concentrated prey resource than northern elephant seals. Despite this, they may be more susceptible to fluctuations in prey availability, for example related to climatic change (Testa *et al.* 1991). In extreme contrast is the very conservative pattern of growth (at least to 8 months of age) of northern elephant seals, which may be a consequence of less predictable and/or more dispersed prey. Juvenile survival in northern elephant seals appears to be unrelated to body condition and size (Le Boeuf *et al.* 1994). Instead, if prey are more scattered, chance may be important in finding a resource-rich area to exploit. If so, more energy would be expended searching, less energy would be available for growth and consequently, mass increases would be negligible. As a result, growth rate and body size are a trade-off for the poorer foraging conditions. Such a contrast in growth is strong evidence that prey of both elephant seal species may differ with respect to abundance, location in the water column or quality. Increased growth rates and body size have been associated with improved nutrition in terrestrial mammals (Ozoga and Verme 1982; Solberg and Saether 1994), and this may partly explain the observed difference between the two species of elephant seals. Periodic changes in marine ecosystems (*e.g.* Testa *et al.* 1991; Trites and Bigg 1992) may result in interannual variations in energy content of prey for example (Worthy 1987; Martensson *et al.* 1996), and need to be accounted for when making such interspecific comparisons. Larger data sets will also enable more reliable comparisons to be made. Nonetheless, first trip growth is quite variable for southern

and northern elephant seals, and may be affected by prey availability.

3.5 Summary.

A longitudinal study of growth of southern elephant seals during their first foraging trip was undertaken at Macquarie Island. On average, body mass increased by 75% while foraging at sea, with individuals growing at 0.34 ± 0.12 kg/day ($n = 64$), and spending 182 ± 51 days ($n = 64$) at sea. Relatively smaller changes in body length were recorded during the same period, suggesting that growth was comprised primarily of adjustments to body composition, rather than increases in gross body size. This may be in response to the functional demands of pelagic life. Body size established early in life (birth mass and departure mass) positively influenced body mass upon return from the first foraging trip. Growth rate, however, was negatively related to departure mass for females, and this is hypothesised to be related to sex differences in body composition, as well as intrasex differences in foraging skills, diving ability and food conversion efficiency. Despite this, there was no detectable age-specific sexual dimorphism in the first year of life, suggesting that both sexes may exploit similar marine resources. Animals that were at sea longer tended to return in better body condition. Interspecific comparison suggested that southern elephant seals grow more than northern elephant seals and this difference may be related to prey abundance and distribution.

CHAPTER FOUR

LIFE-TIME GROWTH AND IMPLICATIONS FOR POPULATION DYNAMICS.

4.1 Introduction.

Significant declines have been recorded in the southern Indian Ocean and Pacific Ocean populations of southern elephant seals during the last 30 to 40 years, including Macquarie Island (Hindell *et al.* 1994b). Although many causes such as predation (Condy *et al.* 1978), competition with other pinniped species (Bester 1988), depletion of resources (*e.g.* Van Aarde 1980; Burton 1986; McCann and Rothery 1988, Giunet *et al.* 1992), competition with fisheries (Bester 1988) and climatic change (*e.g.* Burton 1986; Vergani and Stanganelli 1990; Hindell *et al.* 1994b) have been suggested, the explanation is still unknown and is likely to be multifactorial. However, current evidence points towards either environmental change or equilibration processes following the intense sealing period of last century (Hindell *et al.* 1994b). Finding an explanation is made difficult by the duration of time spent at sea by this species, the long distances travelled whilst foraging and the remoteness of breeding sites.

In contrast to other populations, the South Georgia stock of southern elephant seals has remained stable, despite 60 years of regulated sealing earlier this century (McCann and Rothery 1988; Boyd *et al.* 1996). Previous studies have highlighted considerable differences between the Macquarie Island and South Georgia

populations. These showed that (i) Macquarie Island cows grew slower than South Georgia cows (Carrick *et al.* 1962a); (ii) Macquarie Island cows were older at first breeding (Carrick *et al.* 1962a); and (iii) Macquarie Island cows were smaller in terms of both body mass (Bryden 1968a) and snout-tail length (Carrick *et al.* 1962a; Ling and Bryden 1981). Differences in age at first breeding have since been confirmed (McCann 1985; Hindell 1991), however the differences in body size and growth rate are yet to be validated.

Current explanations for the population decline relate to an equilibration process and/or environmental change. The equilibration hypothesis depicts the population decline as being due to the population returning to pre-sealing levels after having risen to abnormally high levels following the cessation of intense sealing (Hindell 1991; Hindell *et al.* 1994b). With stabilisation of the population, this hypothesis predicts that: (i) somatic growth rates will increase; (ii) adult body size will increase; (iii) age of first breeding for females will decrease; (iv) adult and first year survival will increase; (v) and population size will stabilise at presealing levels. Such changes are consistent with increasing demographic vigour (Eberhardt 1977; Siniff *et al.* 1978; Hanks 1981). It is believed that the Macquarie Island population may have already reached the presealing population size, however the equilibration process may further involve diminishing undershoots and overshoots (Hindell *et al.* 1994b).

The environmental change hypothesis is based on the premise that food resources are “patchily” distributed in time and space, and that abiotic changes in the

environment influence this distribution (Hindell *et al.* 1994b). If environmental change was fluctuating on a relatively short time-scale, then non-directional change in survival, particularly in first year animals, feeding strategies and foraging grounds could be expected (Hindell *et al.* 1994b). If environmental change was occurring on a longer time-scale, then changes in the adult population may also become obvious. If prey abundance and distribution were limited, adult survival and body size would be expected to be reduced (Stewart and Lavigne 1984; Trites and Bigg 1992), and altered foraging behaviour may accompany these changes (Boyd *et al.* 1994b). If environmental change brought about reduced abundance and energy density of prey, then growth parameters of adults would be expected to decrease. If on the other hand, environmental change only reduced prey abundance, then the lowered population density may allow for greater resources per capita, and consequently result in a long-term increase in growth parameters; similar predictions to the equilibration hypothesis.

By studying life-time growth of southern elephant seals, size-related population parameters such as growth rate and adult body size can be quantified, enabling testing of these hypotheses. This however, requires animals of known-age and although an increasing number of known-age animals exist in the Macquarie Island population (Australian Antarctic Division, *unpub. data*), only small numbers of the older age classes fall into this category. Characters such as coat colour, size, skull proportions and suture closure, ossification, and corpora lutea have been used to age mammals, but such methods are laborious and often unreliable (Laws 1952). Laws (1952) first used dental strata to determine age and since then, over 40 species of

mammals, including pinnipeds, have been aged using teeth (Fancy 1980). Several studies have involved southern elephant seals (Laws 1953; Carrick and Ingham 1962c; McCann 1980; Arnborn *et al.* 1992), but none have considered the accuracy of the technique.

The aims of this chapter are firstly to undertake a study of age determination using extracted teeth, so that a larger data set of age-specific growth data is available. This will then be used for a cross-sectional growth study of both the current and previous southern elephant seal populations of Macquarie Island to (i) confirm previous differences believed to exist between the Macquarie Island and South Georgia populations; (ii) clarify current differences between the South Georgia and Macquarie Island populations; (iii) and relate the findings to explanations for the population decline.

4.2 Methods.

4.2.1 General field work.

Work was undertaken between March 1994 and January 1995 to establish growth curves. Subjects included (i) animals of both sex, hauled-out during the 1994 austral winter and (ii) post-lactation and pre-moult cows from the 1994 breeding season. Morphometric data pertaining to cows from the 1995 breeding season were also included in the analysis (M. Hindell, *unpub. data*). The subjects were a combination of known-age animals previously marked by flipper tags and/or flank brands for the current long-term population study at Macquarie Island (H. Burton, *pers. comm.*) and individuals of unknown-age.

During the winter and premoult phases of the study, a daily search was made of the isthmus study area for animals hauled-out in the previous 24 hours. In contrast, the breeding season phase required the random selection of cows from harems in the isthmus study area, at day 23 of their lactation, coinciding with the average duration of lactation period (Carrick *et al.* 1962a). These cows had been identified with paint marks at the time of giving birth.

Depending on the size of the subject, chemical restraint was performed either intramuscularly with a 1:1 zolazepam and tiletamine combination (Baker *et al.* 1990) or intravenously using a combination of ketamine hydrochloride and diazepam (see Slip and Woods 1996), after physically restraining with a canvas head bag. Mass was measured to the nearest kilogram by suspending the anaesthetised seal in a stretcher from an aluminium tripod, using an electronic strain-gauge of 2500 kg capacity. snout-tail length was measured with the animal in ventral recumbency using a glass fibre tape-measure.

4.2.2 Age determination.

Whilst sedated, the lower left incisor was removed using the method described by Arnbom *et al.* (1992). Teeth were stored individually in distilled water. The method of preparing and processing the teeth for counting cementum layers was based on the procedure developed for pilot whales (*Globicephala malaena*) (Donovan *et al.* 1993). Prior to mounting the teeth, the attached connective and soft tissue was

removed with a tooth-brush and warm water. The teeth were mounted in a commercial polyester resin so that they could be cut longitudinally (*i.e.* along the crown-root axis) with a diamond-edged circular saw. The cut was made slightly sagittal to retain the midline section of the tooth. The remaining resin was dissolved by soaking in acetone and the larger section retained for fine sectioning. Sections were placed in Tissue-Tek II cassettes, and then immersed in RDO (active ingredient of hydrochloric acid), a commercial decalcifying agent. Decalcification required approximately 12 hours. Once decalcified (confirmed by when the tooth felt rubbery), teeth were washed in running tap water for 24 hours, and then soaked in 10% formalin for 48 hours. Teeth were then stored in distilled water with a few crystals of thymol as a preservative.

Thin sections (35 microns) were made using a microtome equipped with a freezing stage, with Tissue-Tek O.C.T. Compound as a mounting medium. A reusable microtome blade was used, requiring sharpening after every 5 to 10 teeth. The fine sections were transferred to a gelatine-coated microscope slide (Appendix 2) using a fine paint brush, mounted in DPX mounting medium, and covered with a glass coverslip. Slides were air dried before storage.

Using a polarising light microscope, dental cementum layers were counted by viewing prepared sections at or near the root tip when possible (Mansfield, 1991; Arnbom *et al.* 1992; Stewart *et al.* 1996). One year was assumed to be represented by a translucent and dark band, known as a growth layer group (McCann 1993). A standardised technique of repeat blind readings was used (McCann 1993). If the first

three counts were the same, this was assumed to be the age. Otherwise, a further two readings were made, and the mean and 95% confidence interval were estimated for all five counts. Those readings beyond the confidence interval were assumed to be reading errors and discarded. The median of the remaining counts was taken as the final age of the tooth. For each replicate, the order of samples read was randomised.

4.2.3 Data.

All growth data used in the analysis of the 1994-95 seals were cross-sectional, with any repeated measurements of individuals not included in the data set. Retrospective analysis of female growth data was also undertaken for Macquarie Island (R. Carrick *unpub. data*, made available by H. Burton) and South Georgia (Tables XIII and XIV, Laws 1953).

Much of the extensive data set of Carrick *et al.* (1962a) comprises longitudinal growth data for animals born between 1951 and 1965 (excluding 1956). To ensure it was cross-sectional data and comparable to other data sets, only the data recorded for the last resight for each individual was used. Initially, pre-1960 and post-1960 cohorts were examined separately (*i.e.* corresponding to the year that subject was born), as marked differences in first year survival have been recorded for the two decades (Hindell 1991). There was considerable overlap of the 95% confidence intervals for the pre-1960 and post-1960 models, indicating that there was no apparent difference. Hence, these cohorts were pooled before fitting a Gompertz model (see below). Data from South Georgia (1948-51) (Laws 1953) did not require any subsampling. Prior to analysis, curvilinear length measurements of Laws (1953)

were reduced by 5% to obtain an estimate of snout-tail length (McLaren 1993), as done by Carrick *et al.* (1962a).

4.2.4 Growth analysis.

A Gompertz growth curve was fitted to the female data using a least-squares iterative procedure (SYSTAT 1992). The general formula used for the Gompertz model, as defined by Fitzhugh Jr. (1976), was:

$$L = A\{\exp[-b\exp(-k*age)]\}$$

where L is ventral recumbency snout-tail length (m), age is measured in months, A is the asymptotic value for body length, b is a scaling parameter (the constant of integration), and k is the growth rate constant (a function of the ratio of maximum growth rate to mature size).

Growth curves were compared by examination of the degree of overlap of 95% confidence intervals. If intervals overlapped, it was assumed that there was no significant difference between curves. The growth of males of polygynous species, such as southern elephant seals, is best described by a double sigmoid growth curve, with separate growth curves for individuals under and over 4 years old (McLaren 1993). For the current Macquarie Island data however, growth functions (Gompertz and von Bertalanffy) could not be fitted to the male data. Instead, a linear regression model was fitted.

Values are presented as mean \pm 1 standard deviation, unless otherwise stated.

4.3 Results.

4.3.1 Age determination.

A total of 126 seals were aged by cementum layers. A further twelve animals of known-age status were sampled: 6 cows (4 to 7 years of age), 1 non-breeding female (4 years of age) and 5 juvenile males (3 to 6 years of age). Repeat blind counts ($n = 5$) of each known-age tooth ($n = 12$) resulted in only 3 (25%) being consistently aged correctly. However, a paired t -test revealed a mean difference of 0.0 ± 1.3 years ($t_{11} = 0$, $P = 1.0$) between estimated and known-age. There was a significant positive relationship between real age and difference (known age - estimated age) ($y = 0.85x + 4.7$; $F_{1,10} = 34.27$, $P < 0.001$, $r^2 = 0.75$), that is animals younger than 4.7 years of age were overestimated and animals older than 4.7 years were underestimated. The age structure of aged individuals is tabulated in Table 4.1a.

The variability of repeat counts of unknown-age teeth was generally consistent, with a mean 95% confidence interval of 0.8 ± 0.7 years ($n = 126$). Of the unknown-age animals ($n = 126$), five had been previously observed on Macquarie Island. Age estimated by cementum layers for 4 of these animals coincided correctly with visual age estimations made at previous sightings (Australian Antarctic Division, *unpub. data*). The other animal was estimated to be 4 years old in 1990, whilst our estimation by cementum layers was 3 years in 1994, the two estimates clearly inconsistent.

Table 4.1. Age structure for subjects (a) that were aged using teeth and (b) used for growth models (known and estimated ages) .

(a)

Age (years)	Number of animals aged using cementum layers	
	Female	Male
0 - 1.0	1	-
1.1 - 2.0	2	2
2.1 - 3.0	4	1
3.1 - 4.0	29	6
4.1 - 5.0	24	-
5.1 - 6.0	18	-
6.1 - 7.0	10	-
7.1 - 8.0	6	-
8.1 - 9.0	7	-
9.1 - 10.0	3	-
10.1 - 11.0	1	-
11.1 - 12.0	3	-
12.1 - 13.0	2	-
13.1 - 14.0	3	-
14.1 - 15.0	4	-
Total	117	9

(b)

Age (years)	Total number of animals	
	Female	Male
0 - 1.0	-	-
1.1 - 2.0	17	24
2.1 - 3.0	6	3
3.1 - 4.0	31	12
4.1 - 5.0	24	-
5.1 - 6.0	18	-
6.1 - 7.0	10	-
7.1 - 8.0	6	-
8.1 - 9.0	7	-
9.1 - 10.0	3	-
10.1 - 11.0	1	-
11.1 - 12.0	3	-
12.1 - 13.0	2	-
13.1 - 14.0	3	-
14.1 - 15.0	4	-
Total	137	39

4.3.2 Growth of females.

4.3.2.1 Macquarie Island, 1994 to 1995.

The snout-tail length of 137 females between 1 and 15 years of age was used to determine growth curves. For 85% ($n = 116$) of these individuals, age was determined using dental cementum layers; the remaining 21 were known-age animals generally less than 2 years of age. Table 4.1b shows the age distribution of animals in this study. Figure 4.1 illustrates the growth curve of females up to 15 years of age for the 1994-95 Macquarie Island population. There was considerable variation in age-specific length particularly in the first 4 to 6 years of life, although this was reduced in the later years of life (Table 4.2). The most rapid growth appears to occur in the second and third years of life. Growth then gradually slows until the asymptotic length (\pm SE) of 2.57 ± 0.03 m is reached at 9 years of age (Table 4.2).

4.3.2.2 Macquarie Island, 1951 to 1965.

Figure 4.2 shows the Gompertz growth curve fitted to the extensive Macquarie Island data set for 1951-65 cohorts. An asymptotic length of 2.39 ± 0.04 m was estimated to be reached at 10 years of age. There was a large degree of variation in age-specific body length, obvious in Figure 4.2.

4.3.2.3 South Georgia, 1948 to 1951.

The 1948-51 South Georgia population was estimated to have an asymptotic length of 2.69 ± 0.05 m, at an age of 17 years (Figure 4.3).

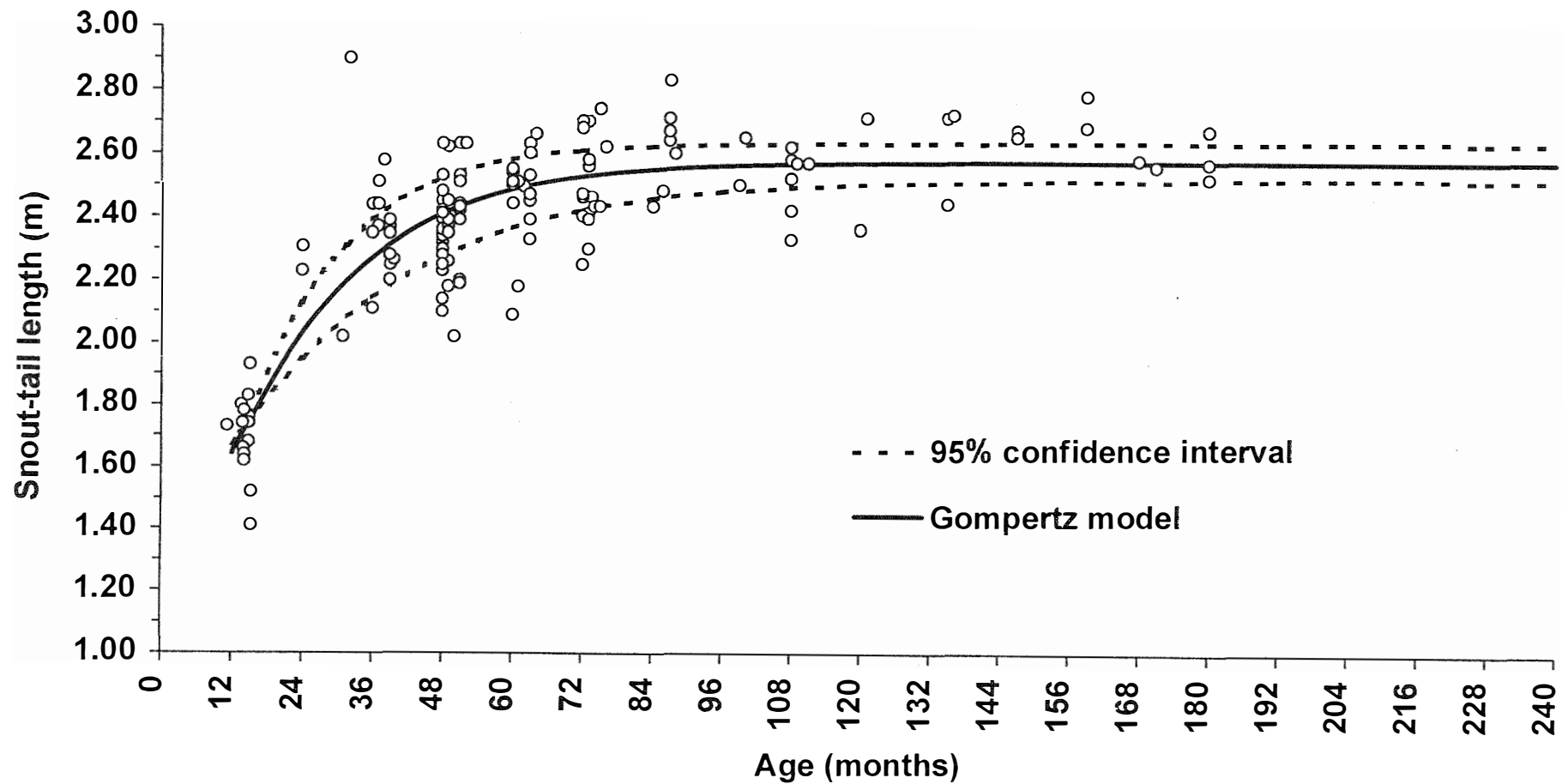


Figure 4.1. Gompertz growth curve and data for the 1994 to 1995 Macquarie Island female elephant seal population (post-one year of age).
 $STL = 2.57\{\exp[-0.85*\exp(-0.05*age)]\}.$

Table 4.2. Snout-tail lengths recorded for female age classes^a, and those predicted using the Gompertz model for the 1994-95 Macquarie Island population.

Age ^b (years)	<i>n</i>	Range	Mean STL \pm SE (m)	Predicted STL \pm SE (m)
1	15	1.41 - 1.93	1.71 \pm 0.03	1.64 \pm 0.03
2	4	2.02 - 2.90	2.37 \pm 0.19	2.03 \pm 0.03
3	15	2.11 - 2.58	2.33 \pm 0.03	2.27 \pm 0.03
4	38	2.02 - 2.63	2.38 \pm 0.02	2.41 \pm 0.03
5	18	2.09 - 2.66	2.47 \pm 0.03	2.48 \pm 0.03
6	18	2.25 - 2.74	2.52 \pm 0.04	2.53 \pm 0.03
7	7	2.43 - 2.83	2.62 \pm 0.14	2.55 \pm 0.03
8	2	2.50 - 2.65	2.58 \pm 0.07	2.56 \pm 0.03
9	7	2.33 - 2.62	2.52 \pm 0.04	2.57 \pm 0.03
10	2	2.36 - 2.71	2.54 \pm 0.08	2.57 \pm 0.03
11	3	2.44 - 2.72	2.62 \pm 0.09	2.57 \pm 0.03
12	2	2.65 - 2.67	2.66 \pm 0.01	2.57 \pm 0.03
13	2	2.68 - 2.78	2.73 \pm 0.05	2.57 \pm 0.03
14	2	2.56 - 2.58	2.57 \pm 0.01	2.57 \pm 0.03
15	3	2.52 - 2.67	2.59 \pm 0.04	2.57 \pm 0.03

^a No age class 0 appears as this played no part in constructing the growth curve (see Figure 4.2).

^b Age classes pertains to animals with that integer value, (*e.g.* age class 1 are animals 1.0 to 1.9 years old, etc), except for age class 0 which is only newborn animals.

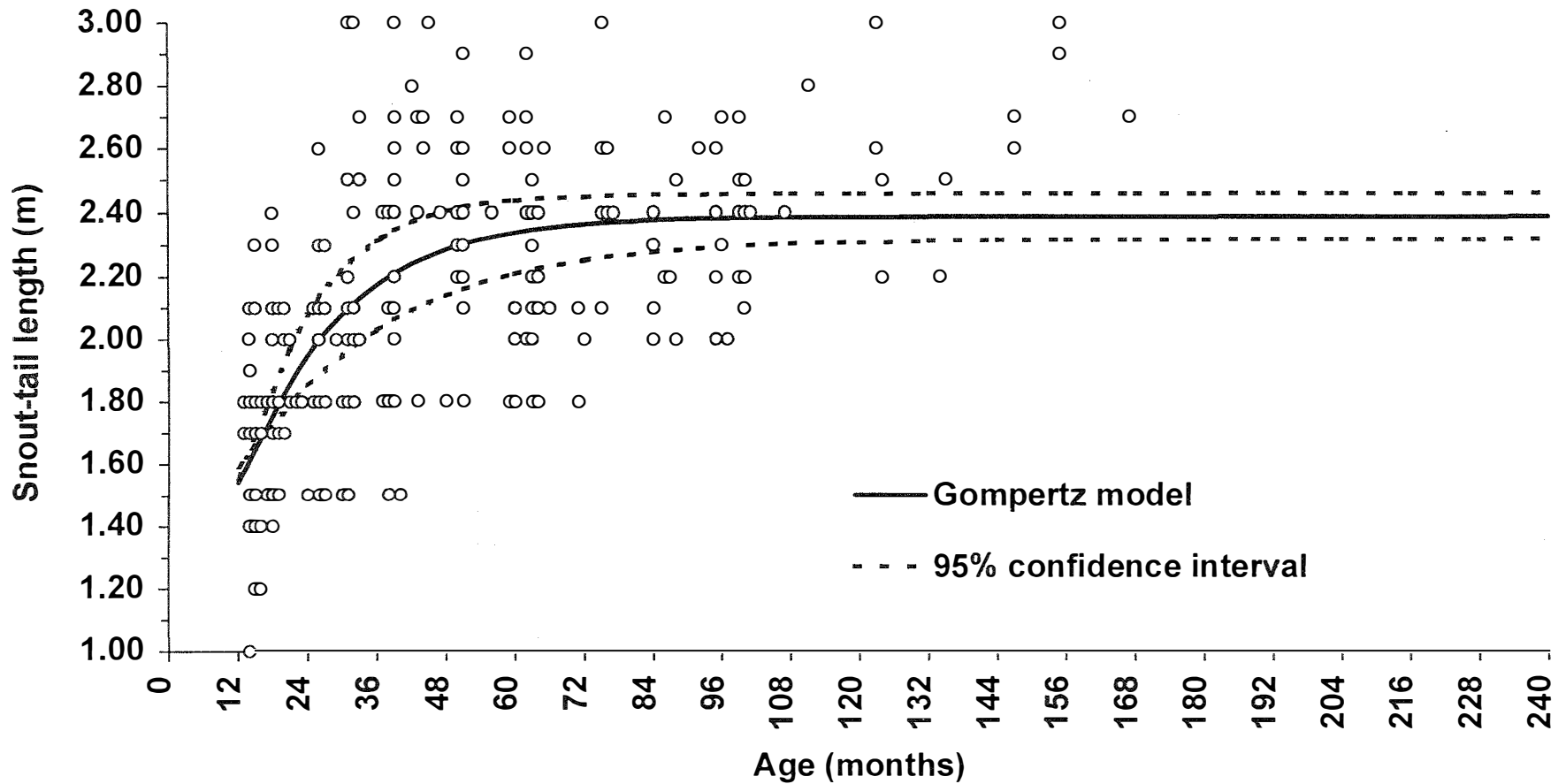


Figure 4.2. Gompertz growth curve and data for the 1951 to 1965 Macquarie Island female elephant seal population (post-one year of age). Data from R. Carrick (*unpub. data*). $STL = 2.39\{\exp[-0.94*\exp(-0.06*age)]\}$.

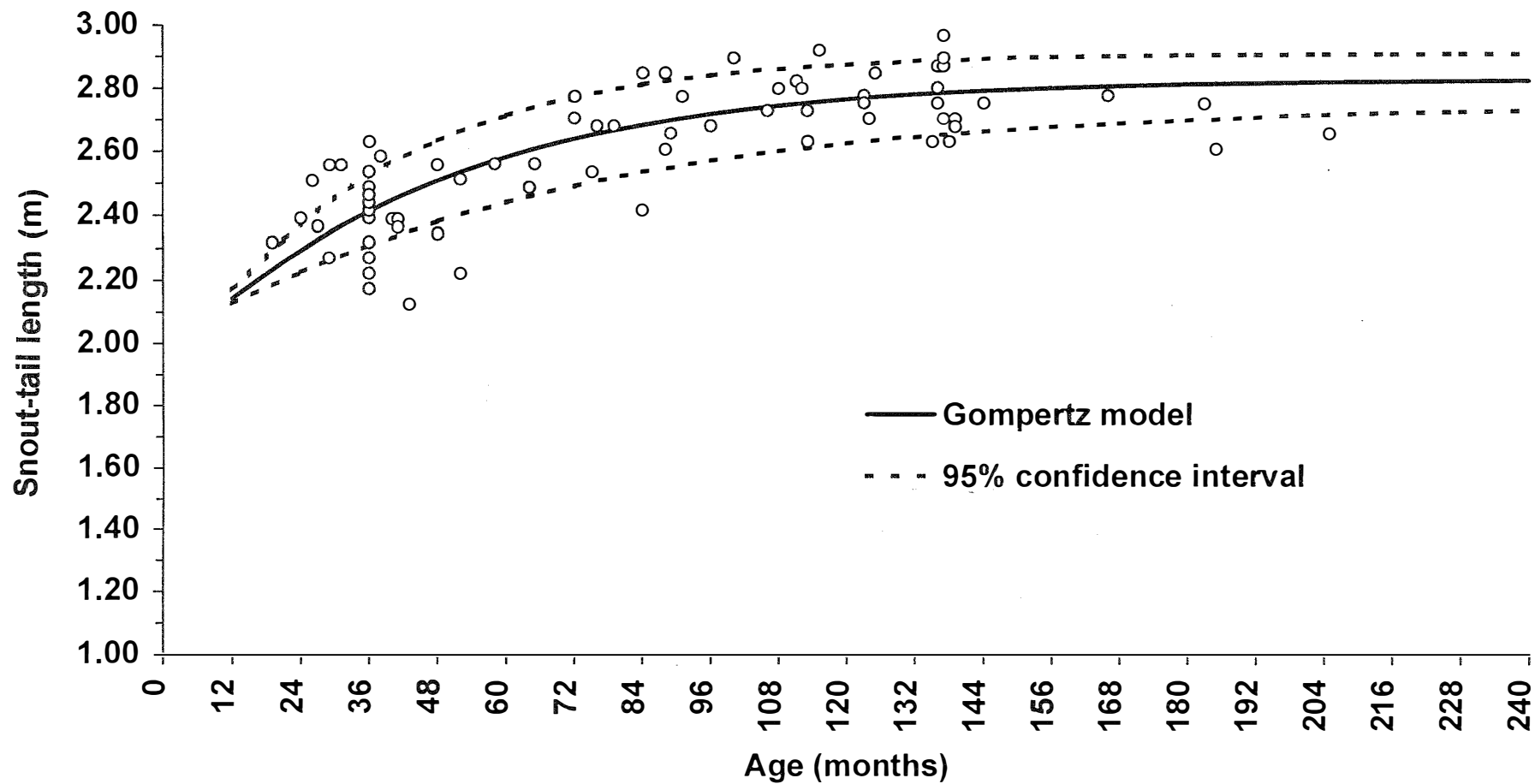


Figure 4.3. Gompertz growth curve and data for the 1948 to 1951 South Georgia female elephant seal population (post-one year of age). Data from Laws (1953). $STL = 2.69\{\exp[-0.35 \cdot \exp(-0.02 \cdot \text{age})]\}$.

4.3.2.4 Macquarie Island, temporal changes.

A significant temporal difference (0.18 m) in adult female body length was noted for Macquarie Island elephant seals between 1994-95 and 1951-65 (Figure 4.4a, Table 4.3). It would appear that both female growth rate and terminal body length have increased over the last 30 to 40 years, although there was no detectable size difference until approximately 8 years of age.

4.3.2.5 Previous interpopulation differences.

There was an obvious difference in the shape of growth curves between South Georgia (1948-51) and Macquarie Island (1951-65 and 1994-95) populations, with growth in the first 4 to 5 years of life appearing to be more rapid at Macquarie Island (Figure 4.4b). There was no overlap of the 95% confidence intervals for asymptotic length for South Georgia (1948-51) and Macquarie Island (1951-65) (Table 4.3, Figure 4.4b), indicating that South Georgia cows were significantly longer in the 1950s and 60s by approximately 0.30 m than those from Macquarie Island (Table 4.3).

4.3.2.6 Current interpopulation differences.

Assuming no temporal changes have occurred with respect to growth rates at South Georgia (McCann 1980), then comparison with the 1994-95 Macquarie Island growth curve suggests that adult females of both populations are not significantly different in body length now (Figure 4.4c).

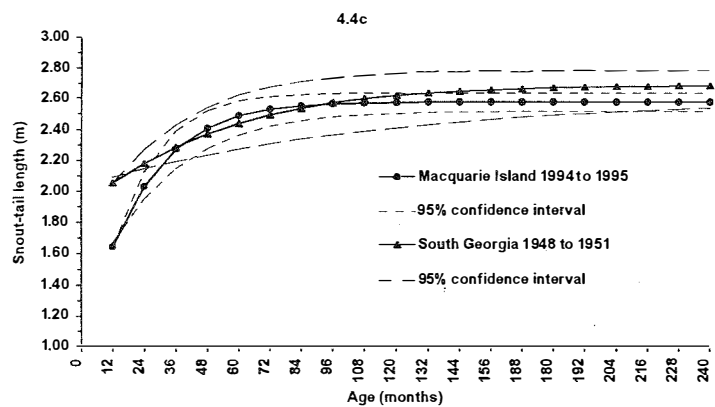
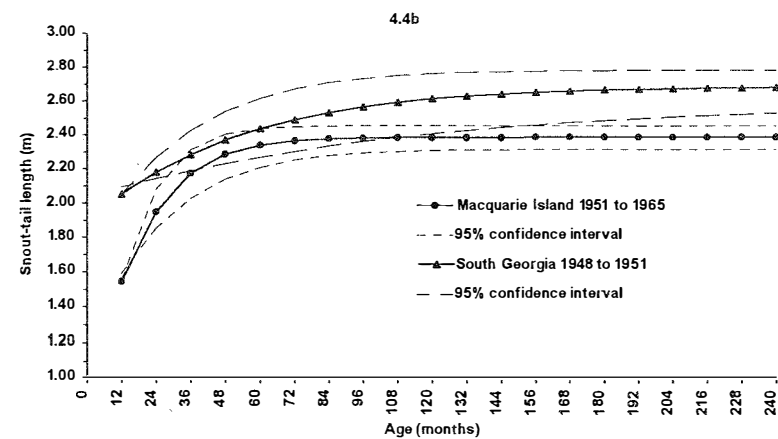
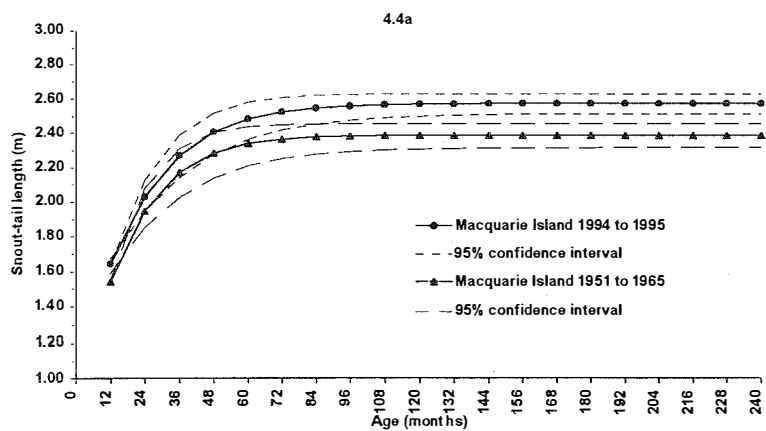


Figure 4.4. Predicted Gompertz growth curves and 95% confidence intervals for temporal and spatial comparison.

Table 4.3. Gompertz growth model parameters, associated standard errors (SE), and 95% confidence interval range for asymptotic length of adult females.

Site	Years	r^2	n	$A \pm \text{SE}$	Confidence range for A	$b \pm \text{SE}$	$k \pm \text{SE}$	Data source
MI	1994-95	0.72	137	2.57 ± 0.03	2.52 - 2.63	0.85 ± 0.10	0.05 ± 0.01	Present study
MI	1951-65	0.45	339	2.39 ± 0.04	2.32 - 2.46	0.94 ± 0.16	0.06 ± 0.01	R. Carrick (<i>unpub. data</i>)
SG	1948-51	0.57	76	2.69 ± 0.05	2.59 - 2.79	0.35 ± 0.05	0.02 ± 0.01	Laws (1953)

4.3.3 Growth of males.

Age-specific body length data from 39 males between 1 and 4 years of age was best described by a linear regression (Figure 4.5). Twenty three percent ($n = 9$) of these animals were aged by dental cementum layers (Table 4.1a). The significant linear relationship ($y = 0.02x + 1.49$; $F_{1,37} = 91.45$, $P < 0.001$, $r^2 = 0.70$) predicted that a 4 year old would have a snout-tail length (\pm SE) of 2.36 ± 0.15 m, comparable to a female of the same age. Snout-tail length at 4 years of age was estimated using a similar method for the 1951-65 Macquarie Island ($F_{1,632} = 466.84$, $P < 0.001$, $r^2 = 0.42$) and South Georgia (1948-51: $F_{1,26} = 48.95$, $P < 0.001$, $r^2 = 0.64$) populations (Table 4.4). There was overlap of confidence intervals for all three groups, suggesting no temporal or inter-population differences exist for males at 4 years of age.

4.4 Discussion.

4.4.1 Age determination.

Age estimation of southern elephant seals has previously used counts of dentine layers (*e.g.* Laws 1952; Carrick and Ingham 1962c). These studies relied on canine teeth collected from dead individuals, the pulp cavity of such teeth remaining open throughout life (McCann 1993). However, there are significant drawbacks with collecting teeth from dead animals, scientifically, practically and ethically (Arnbom *et al.* 1992). For these reasons, Arnbom *et al.* (1992) successfully removed incisor teeth from live southern elephant seals, although the accuracy of this study was not

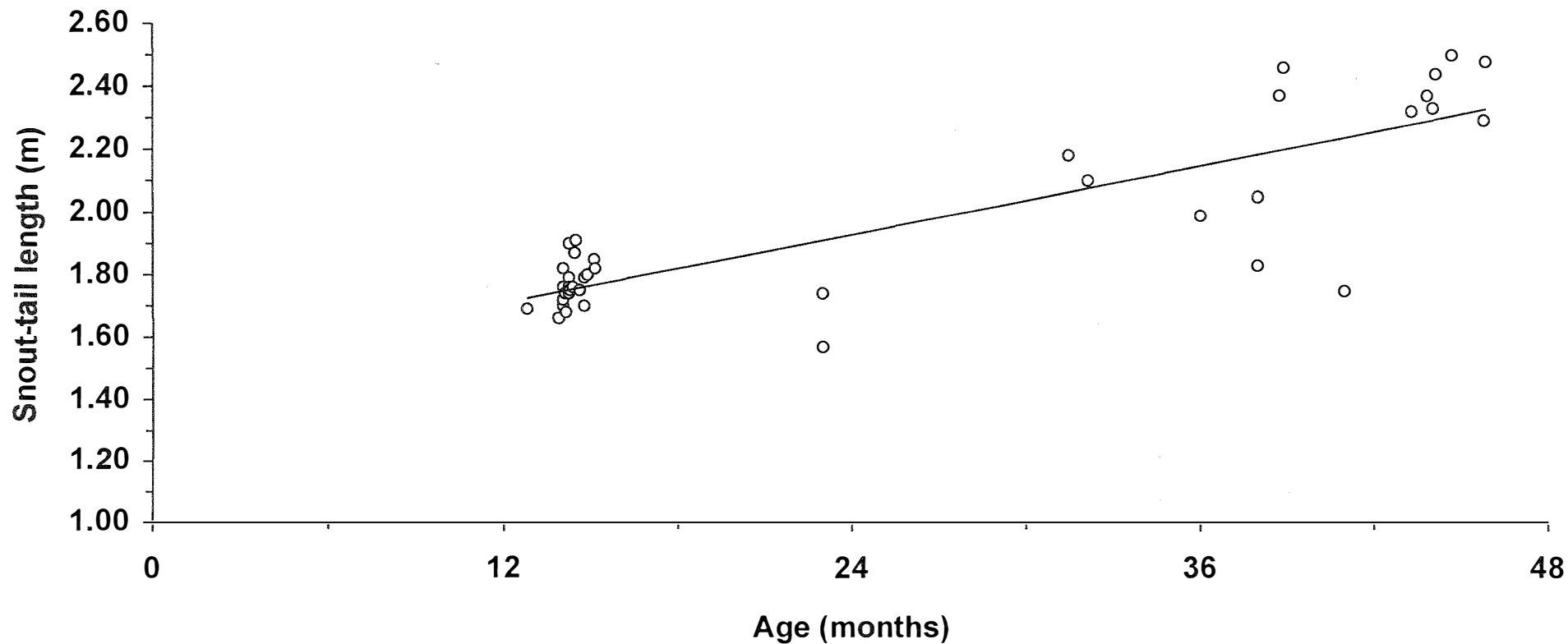


Table 4.4. Estimated snout-tail length (STL) of 4 year old males, calculated using a linear model.

Location	Years	STL \pm SE (m)	95% confidence range (m)	Data source
Macquarie Island	1994-95	2.36 \pm 0.15	2.01 - 2.71	Present study
Macquarie Island	1951-65	2.51 \pm 0.30	1.82 - 3.20	R. Carrick (<i>unpub. data</i>)
South Georgia	1948-51	2.75 \pm 0.16	2.36 - 3.14	Laws (1953)

estimated because known-age animals were not included. For these teeth, the pulp cavity was found to close at 5 to 6 years of age, necessitating counting of cementum layers which are deposited indefinitely on the outer surface of the tooth (Arnbom *et al.* 1992; McCann 1993). Cementum layer counts have also been used to determine the age of northern elephant seals (Klevezal' and Stewart 1994), grey seals (Mansfield 1991; Brent *et al.* 1996), ringed seals (*Phoca hispida*) (Stewart *et al.* 1996) and Antarctic fur seals (Payne 1978; Arnbom *et al.* 1992).

Several sources of variation exist for counts of cementum layers. Brent *et al.* (1996) noted that false annuli may be present, whilst Mansfield (1991) and Klevezal' and Stewart (1994) suggested that the innermost layers may be misinterpreted because they can be subdivided into one or more additional layers. Further, Klevezal' and Stewart (1994) observed a transition of 2 growth layer groups being deposited per year to 1 deposited per year at 2 to 5 years of age in northern elephant seal cows. This may explain the tendency to overestimate the age of younger animals in this study.

Conversely, older animals were underestimated by Brent *et al.* (1996), as in this study. That outer layers of older teeth are more difficult to interpret because they become increasingly narrow with age (Mansfield 1991) may be reason for layers to be missed. Dentine layers also become increasingly difficult to interpret with age in harp seals (Lawson *et al.* 1992). Mansfield (1991) found that accuracy was best in the middle range of years (3-6 years) when annuli were relatively wide and well defined, corresponding with findings of this study.

Underestimation of older age-classes may be a potential source of error when using teeth-aged animals in growth studies. This was tested by two means: (i) by removing all the animals from the data set that were aged using teeth, and then fitting a Gompertz model to the data; and (ii) correcting for this underestimation by adding firstly 1 and then 2 years of age, to animals older than 3 years of age (animals less than or equal to 3 years of age were not adjusted as the majority were of known-age (Table 4.1)). Table 4.5 depicts the Gompertz model parameters after these changes were made. Confidence intervals and standard errors for model parameters were of similar value, although when only known-age animals were used, the standard error and confidence intervals were larger. As there was significant overlap in the confidence interval for the asymptotic body length, underestimation by 1 to 2 years of age appears to make little difference to the Gompertz model parameters. In contrast, the point of inflection for growth curves would presumably be shifted to the left. Although this has no effect on the asymptotic length, it would distort length estimates during the earlier years of life.

Many other factors may introduce bias when using dental layers for age determination, particularly when teeth of the same age can vary in structure (McCann 1993). Compared with canine teeth there is less space between the dental layers of incisors, making reading of growth layers groups more difficult (Brent *et al.* 1996). Further, variation may exist in the age at which the first cementum layer is deposited (Payne 1978). To fully describe the accuracy of age determination, this type of variation needs to be quantified using a large sample of known-age material and tetracycline marking for example (McCann 1993). Large variations have been

Table 4.5. Effect of correcting for underestimation of age and using known-age animals only on female Gompertz model parameters.

Correction factor	A \pm SE	95% confidence interval for A	B \pm SE	K \pm SE	<i>n</i>
Non-adjusted data	2.57 \pm 0.03	2.52 - 2.63	0.85 \pm 0.10	0.05 \pm 0.01	137
+ 1 year ^a	2.58 \pm 0.04	2.51 - 2.65	0.68 \pm 0.07	0.04 \pm 0.01	137
+ 2 year ^a	2.59 \pm 0.04	2.51 - 2.67	0.59 \pm 0.05	0.03 \pm 0.01	137
Known-age data only	2.44 \pm 0.12	2.19 - 2.70	1.75 \pm 1.50	0.12 \pm 0.06	21

^a Only animals older than 3 years of age were adjusted.

recorded in the time of year when the new layer of cementum actually starts being deposited (Mansfield 1991). Deposition may signify the metabolic shift that occurs in spring with the intensive period of breeding, moulting and fasting, hence representing a “birthday” (Stewart *et al.* 1996).

Reader experience is also important. Lawson *et al.* (1992) found increasing accuracy to be associated with experience. In contrast, similar accuracies to this study have been noted between the least experienced and very experienced readers, which may be due to the least experienced reader being trained and familiarised immediately before starting the work (Brent *et al.* 1996). In the present study, intensive practice on randomly selected teeth was undertaken. Accuracy may have been further improved by using several readers, although the mean difference between estimated and actual age reported in this study was the same as that of an experienced reader in the study by Lawson *et al.* (1992), although it was associated with a larger standard deviation.

4.4.2 Adult body size.

4.4.2.1 Suitability of Gompertz growth models.

There are numerous sigmoidal equations that can be fitted to mammalian growth data (Fitzhugh Jr. 1976; Zullinger *et al.* 1984). Gompertz models tend to predict intermediate values for asymptotic value, maximum growth rate and position of inflection point when compared with logistic and von Bertalanffy models, however such biases become less important with larger data sets (Zullinger *et al.* 1984). As Gompertz models make the best compromise, and that other pinniped studies have

used them (*e.g.* Boyd *et al.* 1994a; Hammill *et al.* 1995) they were chosen for this study.

Individuals less than one year of age were not included in the data set because the Gompertz model may have been influenced by the rapid preweaning growth that occurs in such a short period (*e.g.* Little *et al.* 1987; Guinet 1991; Hindell *et al.* 1994c). It is recommended to refer to other sources for length at birth and weaning (*e.g.* Condy 1980; Little *et al.* 1987) and Chapter 3 for models pertaining to growth during the first year of life.

4.4.2.2 Adult size of southern elephant seals.

Somatic growth of female southern elephant seals at Macquarie Island appears to have increased since the 1950s, as a significant difference was found to exist between the asymptotic length of the 1951-65 cohorts and the 1994-95 population. Problems with the data however need to be emphasised. The data used in this study for the 1951-65 analysis included many visual estimates of body length, which could not be distinguished from actual measurements in the original data set. McLaren (1993) used data from the 1951-65 study pertaining only to subjects physically measured ($n = 31$), and estimated a considerably higher asymptotic length with a larger standard error (Table 4.6) and 95% confidence interval (1.79 to 3.75 m) which overlapped with the 1951-65 estimate of this study (2.32 to 2.46 m) and therefore was not considered to be significantly different. The data used by McLaren (1993) was only from the first 10 years of the complete 3 decades of resights (Hindell 1991). McLaren suggested that his large standard error was a result of a

Table 4.6. Comparison of asymptotic snout-tail lengths (STL) between South Georgia and Macquarie Island adult females.

Population	Years	<i>n</i>	STL \pm SE	Model fitted	Author
South Georgia ^a	1948-51	?	2.66	Gompertz	Boyd <i>et al.</i> (1994a) ^b
South Georgia ^a	1948-51	77	2.82 \pm 0.04	von Bertalanffy	McLaren (1993) ^c
South Georgia ^a	1948-51	76	2.69 \pm 0.05	Gompertz	Present study
Macquarie Island ^d	1951-65	31	2.77 \pm 0.43	von Bertalanffy	McLaren (1993)
Macquarie Island ^d	1951-65	339	2.39 \pm 0.04	Gompertz	Present study
Macquarie Island	1994-95	137	2.57 \pm 0.03	Gompertz	Present study

^a Data from Laws (1953).

^b Table 6.1 lists curvilinear nose-tail measurements, however these are actually snout-tail lengths estimated by 90% of curvilinear measurements (I. Boyd, *pers. comm.*). No standard errors were provided.

^c Measurements were converted by reducing the dorsal curvature nose-tail length by 5% to obtain snout-tail length.

^d Data from R. Carrick (*unpub. data*).

small sample size with restricted ages (less than 9 years), hence was very cautious in making a definite conclusion from the data. In contrast, the relatively larger data set used in this study included animals up to 14 years of age. Presumably, an extensive data set would compensate for any small reading errors sustained when making visual estimates of body length.

As male data were limited to the younger age classes, few comments on overall male growth can be made. It does not seem to have changed at Macquarie Island since the 1950s, and that differences between young males in the 1950s at Macquarie Island and South Georgia were negligible. However, differences may have existed for asymptotic length. Construction of complete growth curves for males would be both labour intensive and time consuming, considering the size of adult males. Estimates of growth rates from linear models may be biased as mammalian growth is not linear (Zullinger *et al.* 1984), and these biases need to be accounted for when drawing conclusions from such models.

The difference in length of adult females between Macquarie Island (1951-65) and South Georgia (1948-51), as reported by Carrick *et al.* (1962a) and Bryden (1968a), remained after re-analysis of the complete resight data set (Figure 4.4b, Table 4.3). Further, estimates for the present South Georgia population suggest that asymptotic body length is unchanged since 1948-51 (McCann 1980). This increase in size since the 1950s of Macquarie Island females, has now put them at the same size as those of South Georgia (Figure 4.4c), assuming body growth has remained the same as the stable South Georgia population (McCann 1980; Boyd *et al.* 1996). This increase

suggests that the Macquarie Island population could now be experiencing similar foraging conditions to southern elephant seals at South Georgia. Although recent findings suggest that maternal body mass is similar for South Georgia and Macquarie Island, the data sets are of small size for Macquarie Island (Hindell *et al.* 1994a; Hindell and Slip *in press*) or biased towards small and large cows for South Georgia (Arnbom 1994; Arnbom *et al.* 1994). Further data collection needs to be undertaken so that unbiased samples can be used for comparison of body mass.

The asymptotic body length estimation made for South Georgia (1948-51) in this study is almost identical to that of Boyd *et al.* (1994a) but differs greatly from McLaren (1993) (Table 4.6), justifying the need to use the same type of model when making comparisons between data sets. The similarity of asymptotic length predicted by Boyd *et al.* (1994a) and the present study, despite Boyd *et al.* (1994a) reducing the curvilinear measurements of Laws (1953) by 10% to yield straight-line snout-tail length, suggests that using 5 or 10% for a reduction factor makes little difference.

4.4.3 Growth rate.

With increased food availability, growth rate of mammals is expected to increase (Klein 1968; Reimers 1972; Hanks 1981; Ozoga and Verme 1982; Choquenot 1991). Although South Georgian cows are now of similar size as Macquarie Island cows, Figures 4.4c indicates that Macquarie Island cows may grow at a faster rate during the first 3 to 4 years of life. This difference in growth rate may be an artefact when the small number of data points for individuals less than 3 years of age ($n = 7$)

of the South Georgia data set is compared to 23 data points for Macquarie Island (1994-95) and 173 for Macquarie Island (1951-65). A birth length similar to Macquarie Island would be expected, as birth mass is similar for both sites (Arnbom 1994; Hindell and Slip *in press*). If such a change was made to Figures 4.4b and 4.4c then growth rate of South Georgian females would be similar to the 1994-95 Macquarie Island population, but possibly greater than Macquarie Island cohorts from the 1950s and 1960s. This supports the earlier view that Macquarie Island cows grew slower during the 1950s to 1960s (Figure 6, Carrick *et al.* 1962a).

4.4.4 Age at first breeding for females.

That body length has increased at Macquarie Island since the 1950s indirectly suggests that cows may begin breeding at a younger age. Pinnipeds and some other mammals have a critical body size that must be acquired to undergo puberty (Laws 1956b; Laws 1959; Arnbom *et al.* 1994). If abundant food resources are available, then pinniped growth rates may be high (Stewart and Lavigne 1984), allowing the critical mass to be reached sooner. Examples of an earlier onset of breeding with altered resources include crabeater seals (*Lobodon carcinophagus*) and southern hemisphere whales following the termination of whaling which resulted in increased krill (*Euphausia spp.*) availability (Laws 1977; Bengtson and Laws 1985), and harp seal under various degrees of exploitation (Bowen *et al.* 1981). Large terrestrial mammals appear to respond similarly (Ozoga and Verme 1982; Choquenot 1991). Consequently, age at first breeding may be used as an indicator of resource abundance for populations (Bengtson and Laws 1985).

The majority of cows of the South Georgia stock start breeding at 4 years of age (McCann 1985; Arnborn 1994). Age of first breeding for the Macquarie Island 1950s and 1960s cohort was calculated to be 5 to 6 years (Carrick *et al.* 1962a; Hindell 1991). If this current increase in body size at Macquarie Island has resulted in an earlier onset of first breeding, then this would be consistent with increased population vigour (Hanks 1981). An earlier study at South Georgia estimated that most 3 year old cows were breeding (Laws 1960b), but this was later found to be inaccurate by one year due to problems with the age determination technique (McCann 1985). This is further evidence of the necessity of using known-age animals for determining age of first breeding. Confirmation of the age at first breeding obviously needs to be undertaken.

4.4.5 The population decline.

If environmental variation is affecting southern elephant seal populations, then presumably demographic changes would reflect the duration of effect of such changes. For example, relatively short-term, cyclical occurrences (*e.g.* El Niño events) would be expected to show as short-term, non-directional changes in population parameters, such as first year survival (Hindell *et al.* 1994b). Juvenile northern fur seals have shown cyclical fluctuations in growth rate and body condition that could reflect changes in the marine environment such as ocean temperature and currents, but may also indicate fluctuations in prey availability (Trites and Bigg 1992). Crabeater seals, leopard seals (*Hydrurga leptonyx*) and Weddell seals have also displayed cyclic variations in some aspects of their biology for periods of 20 to 40 years, which have been shown to follow the Southern

Oscillation Index, suggesting that large-scale oceanographic variations may occur as a result of El Niño events (Testa *et al.* 1991). Such events may induce migration, higher mortalities, reduced growth rate and reduced reproductive capability of prey species, as was observed for many fish species of the Eastern Pacific following the 1982-83 El Niño (Arntz *et al.* 1991). Krill availability was also extremely poor around South Georgia for one year after two El Niño events in 1984 and 1987, resulting in poor reproductive performance of several krill eating penguins and Antarctic fur seals (Croxall *et al.* 1988). If prey species were affected, elephant seals would be expected to show altered feeding strategies and foraging grounds over relatively short periods of time whilst adapting to these changes (Hindell *et al.* 1994b). Long-term effects on body size for example, would be unlikely if suitable adjustments were made in terms of locating and exploiting new foraging grounds and resources

In contrast, long-term environmental changes would presumably have a directional effect on populations. For example, rising sea surface temperatures have been implicated in the decline of the Campbell Island rockhopper penguin (*Eudyptes chrysocome*) population by 94% over a 40 year period, possibly by inducing a shift in diet composition from primarily euphausiid crustaceans to mainly fish (Cunningham and Moors 1994). The latter half of this century has seen a significant increase in surface temperature for islands of the Southern Ocean (Jacka *et al.* 1984; Allison and Keague 1986; Adamson *et al.* 1988). A decline in marine primary production off the coast of southern California has been linked to rising temperatures and an overall reduction in upwelling and mixing of water (Lange *et*

al. 1990). Further, where 50% reductions in the ozone layer over Antarctica have occurred, with increased subsequent mid-ultraviolet (UVB) radiation exposure, primary productivity has been reduced by 6 to 12% over 6 week periods (Smith *et al.* 1992). Such gradual changes in primary productivity would presumably have a negative effect on quantity, distribution and caloric density of prey species.

Although there is widespread documentation of climate change in the Southern Ocean, no direct causal relationship has been proven between this and declining animal populations.

The nature of demographic changes observed in the southern elephant seal population at Macquarie Island since the 1950s, primarily increased adult female body length and population decline, suggests that short-term environmental fluctuations have not been the cause. Since 1949, surface air temperatures at Macquarie Island have risen 1°C, twice the global average, a marked increase considering that mean temperature for Macquarie Island is 4.8°C (Adamson *et al.* 1988). If a change in diet has resulted for southern elephant seals, as suggested for Campbell Island rockhopper penguins (Cunningham and Moors 1994), then animals would consequently be expected to have either: (i) reduced adult body size and slower growth rates as a result of overall decreased food consumption per capita as observed for harp seals (Stewart and Lavigne 1984); or (ii) increased adult body size and growth rate because of reduced population density (*e.g.* Reimers 1972; Choquenot 1991; Trites and Bigg 1992). The increased adult body size detected in this study would suggest that reduced population density, resulting in improved food availability, would be the more likely explanation for the observed increase in cow

size at Macquarie Island. If such widespread changes in the environment were having effect on elephant seal populations, the stable South Georgia population (McCann and Rothery 1988; Boyd *et al.* 1996) presents an interesting comparison. The population at Îles Kerguelen is also believed to have stabilised over the last 10 years, after undergoing a peak in the 1970s and then declining (Guinet *et al.* 1992). Rather than be ‘buffered’ from global environmental change, Boyd *et al.* (1996) believe that growth of the South Georgia population is actually limited by the space available for breeding animals on land rather than environmental factors. Clearly, these populations are not being affected the same way as the Macquarie Island population, along with the declining populations at Marion Island (Bester and Wilkinson 1994) and Îles Crozet (Guinet *et al.* 1992). With the decline of such populations, there has been a simultaneous increase of many southern hemisphere otariid species at rates of up to 15% per annum (Harwood and Rohani 1996), an increase of king penguin (*Aptenodytes patagonicus*) populations at South Georgia, Îles Kerguelen and Macquarie Island (Hindell and Burton 1987), and the South Georgia southern elephant seal population has remained stable. Keeping the complexity of the Southern Ocean ecosystem in perspective, perhaps the effect of rising surface temperatures positively influences some predator-prey relationships and negatively influence others, accounting for declines in some populations and increases in others.

Like environmental change, population ‘overshoots’ are another process which can lower population density. With the initial decrease in population vigour associated with such ‘overshoots’, subsequent demographic changes tend to be decreased

juvenile and adult mortality, decreased age of first breeding and reduced fecundity when the population returns to its previous 'stable' level (Fowler 1981; Skogland 1985). That adult body size has increased for Macquarie Island females and is now equivalent to the stable population of South Georgia (Boyd *et al.* 1996) indicates that the population could have at least reached presealing levels after declining from a population peak in the 1950s (Hindell 1991).

Current evidence suggests that the Macquarie Island population continues to decline at an annual rate of 1.2% (Australian Antarctic Division, *unpub. data*). There are several possible causes of this. Firstly, it may simply be 'undershooting' the presealing level after a population 'overshoot' as suggested by Hindell (1991). Alternatively, a long-term environmental change that has resulted in the decline since the 1950s and subsequent density-dependent demographic changes, may still be having an effect. The explanation is more likely to be multifactorial, possibly a combination of population overshoot and long-term environmental change. Maybe an equilibration process has brought the population back to the presealing level, possibly concurrent with the rapid decline in first year survival during the 1960s (Hindell 1991), with long-term environmental change having a background effect but now a direct effect on the population. In either case, a reduction of southern elephant seals numbers at Macquarie Island has resulted, possibly inducing an increased resource availability per capita. Increased growth and body size do not distinguish between either hypothesis and thus, only limited conclusions can be made on the basis of growth. Complete insight into the cause of the Macquarie Island decline will also require further study of survivorship, fecundity, age at first

breeding, foraging behaviour, diet and the effects of environmental change on marine ecosystems.

4.5 Summary

A cross-sectional growth study of southern elephant seals at Macquarie Island up to 15 years of age was undertaken. Dental cementum layers were counted to estimate the age of some animals. Although animals less than 4.7 years of age tended to be overestimated and animals older than 4.7 years underestimated, underestimation by up to 2 years was shown not to make any significant difference to predicted asymptotic body length. Using a Gompertz growth model, Macquarie Island cows in 1994-95 had a longer asymptotic length than during the 1950s and 1960s. However, Macquarie Island cows are now believed to be of similar size as those at South Georgia and grow at similar rates. Temporal changes at Macquarie Island such as these are consistent with either a population equilibration process or long-term environmental change reducing population density. The explanation for the decline of southern elephant seal numbers at Macquarie Island is likely however, to be multifactorial.

CHAPTER 5

GENERAL DISCUSSION.

This study has described the current growth pattern of the southern elephant seal at Macquarie Island, enabling retrospective comparisons with the Macquarie Island population of the 1950s and 1960s, and also with the South Georgia population. The results have allowed important conclusions to be made with respect to the effect of growth on southern elephant seals, particularly with reference to early development, ecology and population dynamics.

Figure 5.1 summarises factors which may play a role in determining growth of southern elephant seals and emphasises the multifactorial nature of growth. The first three growth phases (foetal, preweaning and postweaning growth) are rigidly defined time periods, whilst first foraging trip ('catch-up' growth) and growth to adult size are less defined in terms of time scale. Central to juvenile growth are maternal energy reserves. Without adequate energy stores, both foetal and preweaning growth are directly affected. Once weaned, maternal energy stores have an indirect effect, primarily in terms of how much blubber the pup has laid down. However, as with all predator-prey systems, the fundamental factor influencing all growth stages is prey abundance and distribution: this is the mainstay of energy flow from mother to offspring. In the Antarctic marine ecosystem, relationships between predator and prey are relatively direct and simple, with often one or two trophic levels between higher vertebrate predators and primary production (Figure 5.2).

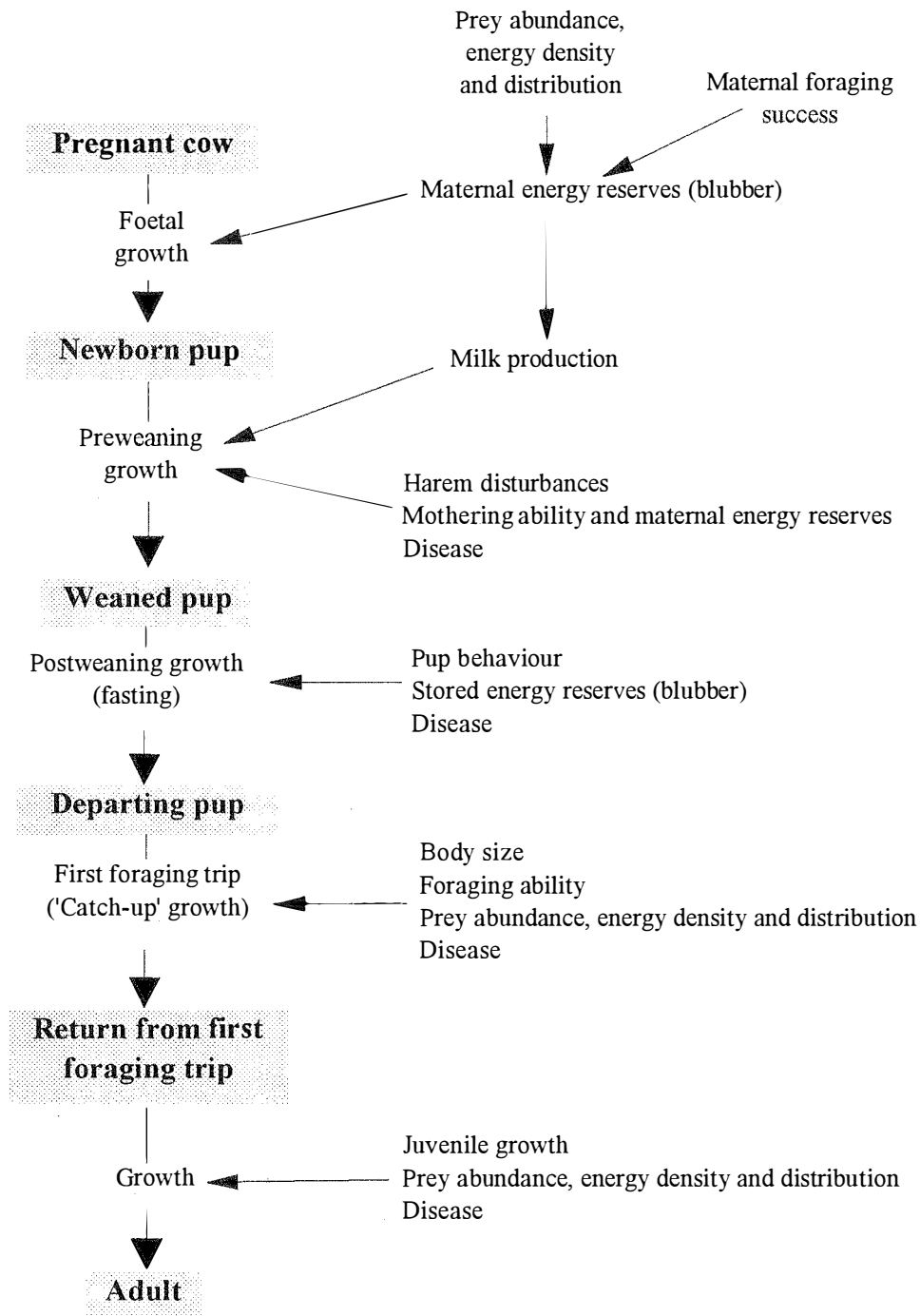


Figure 5.1. Factors potentially affecting growth of southern elephant seals.

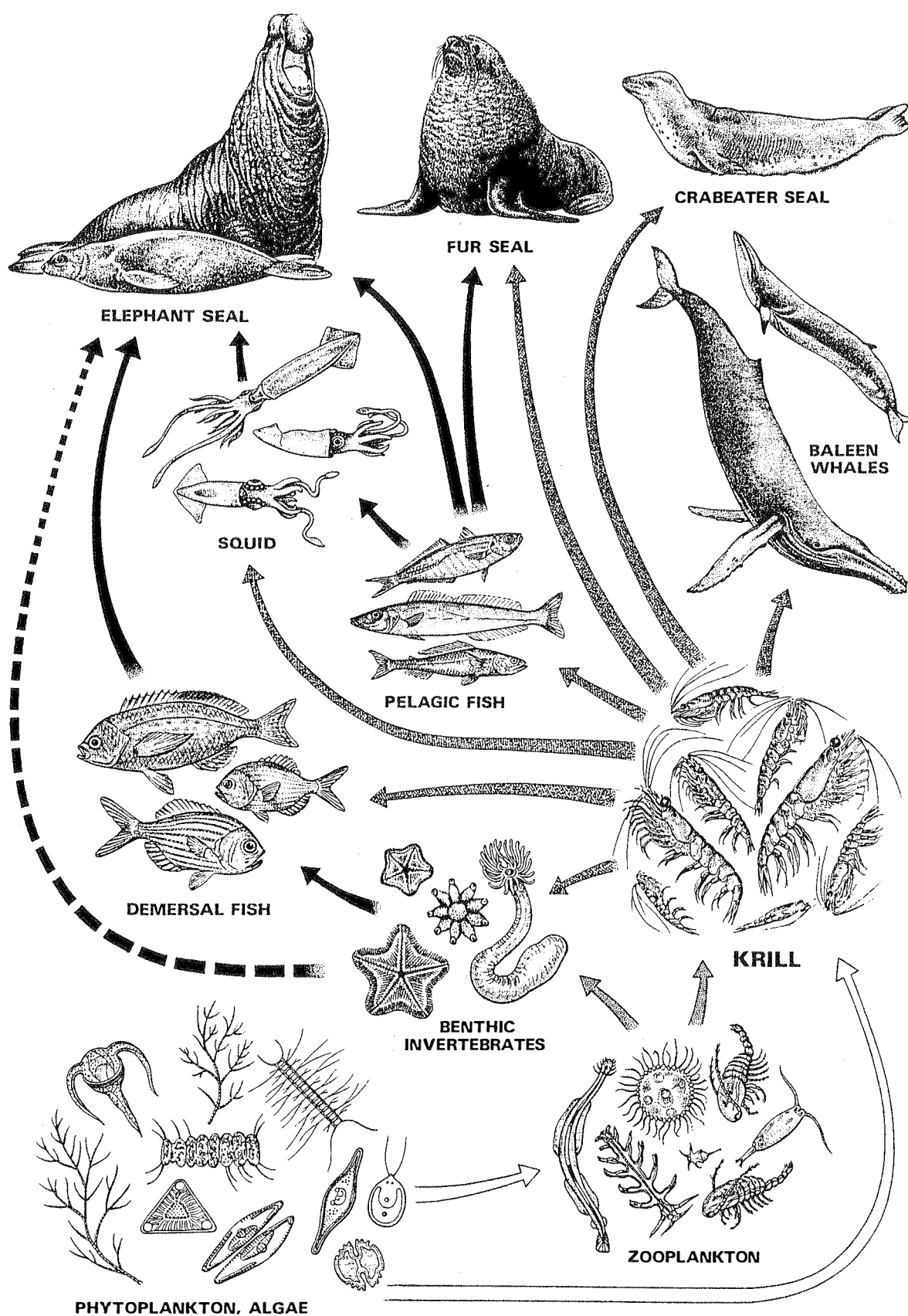


Figure 5.2. Simplified relationship of predators and prey in the Antarctic marine ecosystem (from Bryden 1993). Although not shown, some sea birds, including penguins, are major krill feeders.

Each growth phase will be addressed separately in this chapter, in the context of Figure 5.1. Firstly however, the need for accurate measurement of growth will be emphasised.

5.1 Measurement of growth.

Paramount to growth studies is the ability to undertake accurate and repeatable morphometric measurements. To date, this has not always been the case for pinnipeds. McLaren (1993) reviewed the array of different body length measurements used for pinnipeds. With a large variety of such methods, the need to have standardised methods of measuring morphometrics is apparent (*e.g.* American Society of Mammalogists 1967), as it is not possible to establish a general set of conversions for these different measurements (McLaren 1993). For example, straight-line body measurements made in dorsal recumbency may be longer than in ventral recumbency, because of flexion of the vertebral column (Bonner and Laws 1993). It has been recommended to use straight-line snout-tail length in dorsal recumbency as a standard protocol for Antarctic seals (Bonner and Laws 1993). However, it is easier to measure elephant seals, particularly adult animals, in ventral recumbency because of the difficulty of manually rolling them onto their back. Although curvilinear length measurements have been used previously for elephant seals (*e.g.* Laws 1953; Condy 1980), there may be confusion when trying to convert this to straight-line measurements (Chapter 4). This emphasises the importance of using standardised measurements, particularly when growth data are intended for comparison between both populations or species.

Inaccuracies in individual measurements must be accounted for when calculating average growth curves (Laws 1953). Tape measures constructed of metal or other non-stretch material should be used, as fabric tapes may stretch considerably (Bonner and Laws 1993). Even the length of an individual seal can vary up to 4% between repeat measurements, with further variation as a result of surface-type and positioning of the neck (Chapter 2).

Body length was used in this study to measure life-time growth instead of body mass, primarily to offset the effect of the seasonal fluctuations in physical condition (*i.e.* blubber thickness) of elephant seals (Laws 1953; Bryden 1969b; Gales and Burton 1987). Body length of adult animals is also easier to measure. If necessary, mass can be estimated indirectly using photogrammetry (Chapter 2), however length-mass regressions (*e.g.* Boyd *et al.* 1994a; Chapter 3) may be less time consuming, particularly if an immediate estimation is required. Body mass obtained by direct measurement however, remains essential for energetics, ecological and physiological studies.

In contrast, body mass is a better indicator than body length for growth of elephant seals on their first foraging trip. For this age-class, only a small change in body length was recorded between 5 and 12 months of age, hypothesised to be related to compositional changes rather than a net increase in body size (Chapter 3). This is a crucial phase of life, when important physiological changes take place to enable a transition from terrestrial to marine life (Bryden 1988; Arnborn *et al.* 1993; Thorson and Le Boeuf 1994; Modig 1995; Le Boeuf *et al.* 1996). The first foraging trip may

be a growth phase consisting of maximum growth and consolidation of muscle groups, rather than skeletal growth, enforced by the functional demands of aquatic life (Chapter 3). Further, increased muscle mass has been shown to be important in Weddell seals for optimising body oxygen stores, providing increased aerobic dive limits (Kooyman *et al.* 1983). Because of the proposed nature of body compositional changes during the first foraging trip, body mass is a suitably practical indicator of overall body growth. Techniques such as tritiated water dilution would enable quantification of specific body compositional changes made whilst undertaking the first foraging trip and may provide explanation for how this relates to these growth patterns, as well as dive behaviour (Chapter 3). Knowledge of compositional change may further highlight intersex differences in growth and dive behaviour.

5.2 Foetal growth

Birth mass is a practical measure of prenatal growth or ‘gestational effort’ (Lee *et al.* 1991). It is positively correlated to increasing maternal size and body condition (*i.e.* energy reserves) in southern elephant seals (Campagna *et al.* 1992; Wilkinson 1992; Arnborn *et al.* 1994), and other phocids such as harbour seals (*Phoca vitulina*) (Bowen *et al.* 1994), grey seals (Anderson and Fedak 1987) and harp seals (Stewart and Lavigne 1984). Reduced maternal body condition can alter the growth of mammalian foetuses (Verme 1977) and affect development and function of the cardiovascular system, insulin secretion, lungs and central nervous system (Harding

and Johnston 1995). Reduced maternal energy reserves may also result in lower neonatal growth rates (Woodside *et al.* 1981), ultimately resulting in smaller adult size (Allden 1979).

Maternal energy reserves can be altered by (i) prey abundance, distribution and energy density; (ii) foraging success; and (iii) maternal size. Cows tend to forage either in waters around the Antarctic Convergence or in deep oceanic waters adjacent to the Antarctic Continental Shelf (Hindell *et al.* 1991b; McConnell and Fedak 1996), targeting both fish and cephalopods (Rodhouse *et al.* 1992; Green and Burton 1993; Slip 1995). Foraging success depends on the ability of cows to locate and catch prey, but ultimately availability and energy density of prey determine maternal energy reserves upon return to breeding sites. For example, it is hypothesised that a shift from capelin (*Mallotus villosus*) to Atlantic cod (*Gadus morhua*) as prey species has resulted in a decline in body condition of northwest Atlantic harp seals because Atlantic cod are of reduced energy density (Hammill *et al.* 1995). Interannual variations in birth mass may reflect maternal body condition, which is ultimately determined by food resources (Bryden 1968b; Stewart and Lavigne 1984; Crête *et al.* 1993). Such fluctuations justify the need for long-term studies rather than those undertaken over one breeding season.

5.3 Postnatal, preweaning growth.

5.3.1 Maternal influences: mothering ability and energy reserves.

For mammals in general, larger multiparous females are usually more successful in rearing pups than smaller primiparous cows (Riedman 1990). For elephant seals

this may be because larger cows have more resources available for transfer (*e.g.* Arnbom *et al.* 1994), are socially more dominant (Riedman 1990), may select safer locations within the harem and simply have more mothering experience (Reiter *et al.* 1981).

Maternal condition has an important influence on preweaning growth rate and weaning mass of southern elephant seals (*e.g.* Campagna *et al.* 1992; Arnbom *et al.* 1993; Hindell *et al.* 1994c). Presumably, the larger the cow, the greater the energy reserves she has available for producing a larger pup at weaning (Campagna *et al.* 1992; Arnbom *et al.* 1994). However, the relative amount of energy expended on pups during lactation is quite variable, and is not necessarily related to maternal size (Fedak *et al.* 1996). Considerable differences have been recorded between the weaning mass of pups of large and small cows at Península Valdés (Campagna *et al.* 1992). These variations may reflect the large range reported for maternal post-partum body mass (*i.e.* energy stores) (Arnbom *et al.* 1994) and consequently, the wide variation in age-specific size data demonstrated for both subyearlings and adults (Campagna *et al.* 1992; Arnbom *et al.* 1994; Chapters 3 and 4).

5.3.2 Milk production.

The interrelationship of marine resources, maternal expenditure and growth cannot be overemphasised for pinnipeds. In particular, the availability of food resources may determine how much energy a female can transfer to her pup, in the form of milk (Riedman 1990). The unique growth pattern of elephant seal pups and the necessity of obtaining a thick layer of subcutaneous adipose tissue for thermal

insulation and future growth, partly depends on the quality of milk and how much is obtained.

Apart from the hooded seal (*Cystophora cristata*), phocid pups are generally born with little body fat (Oftedal *et al.* 1993), hence the need for rapid acquisition of subcutaneous fat. Phocid milk typically has a high fat and low water content (Oftedal *et al.* 1993) compared to milk of other mammals which tends to provide most energy in the form of lactose (Carlini *et al.* 1994). Fat concentration of up to 55% have been recorded for southern elephant seals (Hindell *et al.* 1994c). Milk composition may change rapidly immediately prior to weaning, as a result of the mother's energy reserves reaching a critical low point (Hindell *et al.* 1994c). Hence, variable post-partum body condition of cows may also account for the wide range of nursing period observed (18-27 days) (Carrick *et al.* 1962a). Moreover, changes in milk composition may also reflect deposition rate of adipose tissue by pups, perceived as body growth, though weaning mass has not been found to be related to mean fat content of milk (Hindell *et al.* 1994c).

Although studies have considered the quantity of milk produced by elephant seals (Costa *et al.* 1986; Kretzmann *et al.* 1993; Hindell and Slip *in press*), it is difficult to quantify the effect this has on pup growth. Udder morphometrics in bovine cows (*Bos spp.*) and udder weight in red deer hinds are related to body mass and milk/fat yield, suggesting that larger females may be capable of producing more milk than their smaller counterparts (Mitchell *et al.* 1976; Pawlina 1993). More available milk presumably means increased pup intake.

5.3.3 Harem disturbance

Bryden (1968b) recognised a slower growth rate of southern elephant seals at Macquarie Island, compared with South Georgia, and proposed that this resulted from increased harem disturbance which interfered with suckling. Interruption of suckling bouts by social disturbance has been recognised as a cause of increased pup mortality in northern elephant seals, with overcrowding increasing interfemale aggression and subsequently, the chance of mother-pup separation (Le Boeuf *et al.* 1972, Le Boeuf and Briggs 1977).

There is a high incidence of traumatic injuries received by elephant seal pups (Bryden 1968b; Le Boeuf *et al.* 1972; McCann 1982), and these appear to be an important cause of death of other pinniped pups, including grey seals (Anderson *et al.* 1979). Such injuries are a consequence of the high density in elephant seal harems and violent displays of bull dominance (Carrick *et al.* 1962a; Le Boeuf and Briggs 1977; Bester and Lengart 1982). Likewise, cows may be extremely aggressive towards pups (Le Boeuf and Briggs 1977; McCann 1982; Ribic 1988), and were observed during field work for this study biting their own pups. Disease and physical injuries may predispose pups to separation from their mother and/or starvation; this phenomenon is known as the trauma-starvation syndrome and may be a major cause of pup morbidity and mortality (Le Boeuf and Briggs 1977; McCann 1982). Studies of northern elephant seals have shown that a high percentage of pup mortalities were related to this syndrome rather than specific disease entities (Le Boeuf and Briggs 1977). Traumatic injuries may reduce milk intake of pups, retard growth and further

compromise their immune system (Bryden 1968b; Halliday 1980). However, it is difficult to demarcate the effects of infection and malnutrition, as they tend to act synergistically (Halliday 1980).

5.3.4 Disease.

Apart from traumatic injuries, there is no direct evidence in the literature of infectious disease in unweaned elephant seals. Internal parasite burdens have been reported in other pinniped pups including Hawaiian monk seals (*Monoachus schauinslandi*), northern fur seals and Stellar sea lions (Olsen and Lyons 1965; Banish and Gilmartin 1992), however it remains to be seen whether these are the cause of reduced growth rate.

Other disease processes, such as congenital and ocular disorders may affect growth of afflicted elephant seals. Congenital abnormalities have been reported to affect the limbs of several genera of pinnipeds (Liepold 1980). Such deformities would presumably restrict flipper movement and coordination, consequently restricting foraging and retarding growth in later life. Diseased eyes (corneal ulceration, corneal opacities and total ablation) were observed in southern elephant seals during the present study. However, it is uncertain whether this would affect foraging, as blind ringed seals have been observed in healthy body condition (see Riedman 1990).

5.4 Postweaning fast

Behavioural and physiological changes during the postweaning fast, such as development of diving physiology, strengthening of locomotory muscle groups and the learning of foraging techniques may play a key role in determining growth rate in the critical first year, but require further investigation (Bryden, 1969c; Reiter *et al.* 1978; Arnbom *et al.* 1993; Thorsen and Le Boeuf 1994; Modig 1995; Le Boeuf *et al.* 1996). With increased energy stores available for the fast, heavier pups are able to fast longer and still depart relatively heavier than smaller pups, the increased fast duration allowing for greater time to develop swimming and diving skills (Arnbom *et al.* 1993). Postnatal factors during the postweaning fast, such as departure mass, appear to have more influence than prenatal factors (*e.g.* birth mass) on body mass after the first foraging trip, suggesting that development during the postweaning fast is an important determinant in first trip success (Chapter 3).

5.5 First foraging trip.

This study was the first to investigate growth of southern elephant seals during their first foraging trip. Many factors, relating both to the individual and the marine ecosystem may determine growth during this phase of life. Body size attained before departure contributes to success during this foraging trip. For example, both birth and departure mass were positively related to body mass of individuals returning from their first foraging trip (Chapter 3), suggesting that increased body size is advantageous for this aquatic phase. This is confounded however by the finding that smaller animals returned earlier, and consequently, had less foraging time.

Presumably, larger juveniles would be stronger divers and have thermal advantages over smaller counterparts, allowing for more successful foraging and longer periods spent at sea. Although larger body size, for example at weaning, would be expected to enhance first year survival, this is not the case for northern elephant seals in which both light and heavy weaned pups displayed similar survivorship rates (Le Boeuf *et al.* 1994). Estimation of survivorship rates were based on tag resights in this study, and the effect of tag loss may have led to misinterpretation of survivorship rates (Erickson *et al.* 1993; Le Boeuf *et al.* 1994).

The relationship between prey abundance/distribution and dispersal patterns of subyearlings may also be a very important determinant of growth for this age group. The extreme differences observed between first trip growth of southern elephant seals and northern elephant seals described in Chapter 3 may be explained by a difference in prey distribution for the two species, with more predictable and concentrated prey being hypothesised to exist for southern elephant seals. Increased growth rates and body size have also been associated with improved nutrition in terrestrial mammals (Ozoga and Verme 1982; Solberg and Saether 1994).

No studies specifically document the incidence of disease during this phase of life. Mortality rates of up to 98% have been recorded in the first year of life for southern elephant seals, however the actual cause of mortality is unknown (Hindell 1991). Attacks by killer whales, presumed to be a major cause of juvenile mortality of southern elephant seals (Condy *et al.* 1978; Guinet *et al.* 1992), may inflict non-lethal wounds that could severely limit foraging.

5.6 Adult growth.

5.6.1 Influence of juvenile growth.

Body size established early in life can have a long term effect on subsequent body growth in mammals, such as in red deer (Suttie and Hamilton 1983), bighorn sheep, (Festa-Bianchet *et al.* 1996), merino sheep (*Ovis aries*) (Allden 1979), northern fur seals (Baker *et al.* 1994), and rats (*Rattus spp.*) (Berg *et al.* 1963). Therefore, birth and weaning mass may act as indicators not only of first year growth, but also of potential survival and reproductive success at mature ages (Schultz and Johnson 1995). Depressed juvenile growth may not be compensated for by subsequent 'catch-up' growth, preventing mammals from reaching their genetic growth potential (Allden 1979; Suttie and Hamilton 1983). Such a setback for elephant seals could potentially affect long-term reproductive success, as body size may determine this for both males and females (McCann 1981; Deutsch *et al.* 1990; Arnborn 1994; Modig 1996;). It must be emphasised that events beyond the first year of life can also have profound effects on adult body size (Festa-Bianchet *et al.* 1996), as over half of life-time growth occurs beyond 1 year of age for both sexes, particularly for male elephant seals (Chapter 4).

5.6.2 Prey abundance, energy density and distribution.

Once the hindrances of adapting to the marine environment are overcome before and during the first foraging trip, further development of diving physiology of elephant seals can occur (Le Boeuf *et al.* 1996), allowing for more distant foraging grounds to be exploited and the true growth potential of these animals to be more closely achieved. At this stage of life, if all other growth determinants are overcome

and animals can successfully exploit marine resources, the only limiting factors are prey abundance, energy density and distribution.

5.6.3 Disease.

Numerous examples of disease directly reducing growth of mammals exist in the literature, indicating that for optimum growth to occur, the immune system must be functioning normally (see Halliday 1980). Impairment of the immune system may be the underlying cause of disease, and this can be affected by many factors including nutritional status (Chandra and Kumari 1994), environmental pollution (de Swart 1995) and stress (Rabin *et al.* 1989; Khansari *et al.* 1990).

To date, there is no direct evidence that infectious disease plays a part in southern elephant seal population declines (Anonymous 1991). However, there are records of mass mortalities of pinnipeds dating back to 1813 (Harwood and Hall 1990), whilst more recently, epizootics of morbillivirus infection killed thousands of Northern hemisphere phocids during the 1980s (Kennedy 1990). These highlight the need for further research into infectious processes of pinnipeds and their effect on growth and population demographics. There is little information available regarding the role that pathogens play in declining animal populations, however this may reflect the underrating of disease as a factor in population dynamics (Caughley and Gunn 1996).

5.7 Population ecology.

5.7.1 Interpopulation differences in body size.

The observed size difference of southern elephant seal cows at Macquarie Island and South Georgia during the 1950s and 1960s (Chapter 4) could have resulted from (i) genetic variation, (ii) ecological factors (iii) biased sampling or (iv) a combination of these factors.

There is evidence that genetic divergence has occurred in populations of southern elephant seals (Gales *et al.* 1989; Slade *in press*), and this may partly explain the observed differences in length. Evidence that the Macquarie Island population has approached presealing levels (Hindell 1991), and that maternal mass is similar at both sites (Hindell and Slip *in press*), tends to suggest that both populations are exposed to similar foraging conditions now and that the Macquarie Island population has reached its genetic potential for body size. However, the time scale over which this change in body length at Macquarie Island has occurred tends to suggest that cows during the 1950s and 1960s were limited more by the environment (*i.e.* food resources) than genetics.

Temporal or spatial variation in food availability may also explain the length differences (Eberhardt 1977; Siniff *et al.* 1978). The model proposed by Stewart and Lavigne (1984) for harp seals, explains how temporal variations in food availability can reduce maternal body condition. With decreased maternal condition, there is a subsequent reduction in reproductive performance of cows such that: ovulation rates are decreased and oestrus delayed (Woodside *et al.* 1981), pregnancy rate is

decreased (Thomas 1982), foetal resorption is more frequent (Woodside *et al.* 1981), neonatal growth rates are lower (Woodside *et al.* 1981) and resultant adult size is reduced (Allden 1979). Such a model would suggest that similar food resources are currently available for both populations, as both offspring and maternal mass are similar (Hindell *et al.* 1994a; Hindell and Slip *in press*), however there are no data currently available to suggest similarities in food resource availability for the two populations (Burton *et al.* 1997). A reduction in food resources may increase female mortality, subsequently reducing size of adults (Burton *et al.* 1997).

Cows of South Georgia were previously believed to be 16% heavier at 20 years of age, than those at Macquarie Island (Laws 1984). A change in available energy since the 1950s as a result of increased prey abundance or quality may explain why there is now no difference in maternal mass between Macquarie Island and South Georgia (Hindell and Slip *in press*). Reduced prey availability has been implicated in reduced growth rate of Antarctic fur seals (Boyd *et al.* 1994b) as changes at the trophic-level of phytoplankton and zooplankton may subsequently affect higher level consumers such as squid, fish and seals. Prey may also undergo seasonal and interannual changes in energy density (Worthy 1987; Martensson *et al.* 1996). Such changes may be associated with environmental change affecting marine ecosystems. For example, Burton (1986) and Hindell and Burton (1987) hypothesised that altered sea temperatures and atmospheric conditions around Heard Island may have resulted in decreased food availability for juvenile seals.

The data set of Laws (1953) used in the comparison of Macquarie Island and South Georgia (Chapter 4) was biased towards larger animals as the study relied on animals selected by sealers. Further, the assumption that both weaning and maternal mass are now similar for both sites (Hindell and Slip *in press*) is based on a small sample size of Macquarie Island animals and a biased sample for South Georgia, which contained an overrepresentation of large and small cows (Arnbom 1994). In contrast, the selection of breeding cows for this study was completely random (Chapter 4). These types of biases need to be accounted for and indicate that further sampling needs to be undertaken, particularly at South Georgia.

5.7.2 Explanation of the population decline.

This study provides little supporting evidence for a particular reason for the decline, as it does not differentiate between the environmental change and equilibration hypotheses for reasons given in Chapter 4. The most likely scenario is that several factors (may be related both to the environment and population dynamics) are implicated, and these have resulted in changes to the marine resources available to southern elephant seals.

5.8 Further research.

The last decade has seen an abundance of data collected on southern elephant seals, particularly relating to their diet, foraging behaviour and feeding grounds. However, many questions still exist, relating to growth, general ecology and reasons for the population decline.

The indirect effects of altered juvenile growth rate on adult body size, survival rate and population age structure need to be investigated. Reasons for the high first year mortality rate are still unknown. Relating interannual fluctuations in first year growth, foraging behaviour, diet and prey distribution to first year mortality may provide some clues to causal factors. Such data are currently being collected from satellite dive-recorders on first trip elephant seals from Macquarie Island (H. Burton, *pers. comm.*). Data needs to be collected from South Georgia to enable current comparisons between the two sites.

Less obvious determinants of growth also need to be studied. The role of infectious disease needs addressing, possibly by using serological screening, as well as the implications this may have on growth and mortality, particularly in the first few years of life. By examining body compositional changes during the first year of life, the physiological adjustment to pelagic life may be better understood, and how this relates to body growth and dive behaviour is possible. Although sexual dimorphism does not manifest in the first year of life (Chapter 3), differences between the sexes in body composition may develop.

Growth rates can reveal many details about demographic features of populations (Chapter 4) and can be used as an ‘indicator’ for population change. Other demographic ‘indicators’ such as juvenile and adult survival rates and population size were beyond the scope of this study. Analysis of data from the current mark-resight program at Macquarie Island will be the basis of determining such parameters (H. Burton, *pers. comm.*). Verification of the decreased age at first

breeding (Chapter 4) is also needed, and is currently being undertaken at Macquarie Island (C. McMahon, *pers. comm.*). The current long-term mark-recapture program for southern elephant seals at Macquarie Island will also enable conclusions to be made with respect to the effect of changing growth rates on population size and structure.

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Appendix 1

Calculation of a section volume for estimation of body volume.

The sum of all five sections was the total estimated volume of the individual seal.

(VOL = body volume, cone^a = 'parent' cone which contains the section, cone^b = smaller cone which does not include the section.) Refer to Figure 2.1 for a description of the variables.

$$\begin{aligned}\text{section VOL} &= \text{VOL cone}^a - \text{VOL cone}^b \\ &= (\pi * r^2 * d)/3 - [\pi * r^2 * (d-h)]/3\end{aligned}$$

$$\text{where } d = (h * \text{base radius})/(\text{base radius} - \text{roof radius})$$

$$h = (L-K)/5$$

$$\text{cone volume} = (\pi * r^2 * h)/3 ; r = \text{radius}, h = \text{height}.$$

Appendix 2

Microscope slide preparation ('subbing').

Slides were cleaned by soaking in dichromate cleaning solution (100 g potassium dichromate, mixed in 1.0 L of distilled water; then 100 mL of sulphuric acid (neat) added very slowly) for 12 hours. They were then washed in running tap water for 2 to 6 hours, then rinsed in distilled water several times and allowed to then drain well prior to immersing in the subbing solution. It is important that the slides are not allowed to dry between cleaning and coating, as the subbing solution will not properly wet the dried slides (R. Teague *pers. comm.*).

The subbing solution was made by dissolving 5 g of gelatine in 1.0 L of warm distilled water (to make a 5% solution). 0.5 g of chromium potassium sulphate (chrome alum) was then added. After filtering through Whatman #1 filter paper, this solution can be stored at 5°C for 48 hours, but discarded after this. Once dipped in the subbing solution, slides were then allowed to dry vertically in a dust free environment.