

# The role of juvenile foraging ecology and growth in the evolution of life history strategies for southern elephant seals



By  
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June, 2005



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*An immature male southern elephant seal on the Isthmus at Macquarie Island*

### Statement Of Originality

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

Iain Field

Date

### Statement Of Authority Of Access

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Date

## Dedication

To my parents, John and Agnes, for their everlasting and enduring support and encouragement.

# Abstract

In highly dynamic and unpredictable environments such as the Southern Ocean, species that have evolved behaviours that reduce the effects of intra-specific competition may have a selective advantage. This is particularly true when juveniles face disadvantages when foraging due to morphological or physiological limitation, such as in the case of many marine mammals.

Southern elephant seals (*Mirounga leonina*) are a major consumer of biomass in the Southern Ocean with a global distribution. Recent modelling of the Macquarie Island population concluded that juvenile survival is a key parameter in influencing the rates of population change and as an important demographic component of the population. Resource limitation has been suggested as the primary reason for the change in numbers of these populations and this coupled with the importance of juvenile rates of survival influencing population change may provide some insight into explaining any reduction in juvenile survival. Until now, little has been known about these juveniles, ontogenetic and intra-specific differences in life history and foraging ecology have been suggested but not investigated. During this juvenile stage individuals undergo many morphometric and physiological changes as they develop toward maturity. Therefore, it would seem likely that studying the foraging ecology and growth and development patterns of this demographic group may show the proximate processes in affecting population dynamics. This study has followed juvenile seals as they grow and develop rapidly toward adulthood observing changes in foraging areas or strategies and associated changes in prey availability, differences in the seasonal availability of prey, changes in morphology and physiology for growth, maintenance or provisioning toward adulthood. In this thesis I present data for:

1) *Anaesthesia for safe handling* - I assessed the effects of variation in body condition and age at on the characteristics of anaesthesia, including induction time and dose-specific recovery rate which has increased the control over immobilisation level and duration, and reduces handling times for wild pinnipeds.

2) *Foraging range* and 3) *Habitat use of the Southern Ocean* - I tracked the at-sea movements of juvenile southern elephant seals using locations derived from recorded light levels.

4) *Diet* – I describe intra-specific dietary differences in prey composition and size.

5) *Metabolic estimates and energy use* and 6) *Growth and body condition changes* - I examined changes in mass and body composition of juvenile southern elephant seals during and between their annual moult and mid-year haul-outs.

*General discussion* - These key ecological areas of an important predator has increased our understanding of the evolutionary and ecological interactions that influence the population dynamics of southern elephant seals at Macquarie Island and the structure of the Southern Ocean ecosystem.

## Statement of publication and co-authorship

Publications produced as part of this thesis:

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Mark Hindell  
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Alistair Richardson  
(Head Of School)

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## General Introduction

## Life history strategies

Life history studies are fundamental for understanding the ‘how’ and ‘why’ of individual behaviour (Boness et al. 2002), but they also (and possibly more importantly) provide an understanding of the actions of natural selection that underpin all biological studies (Fisher 1958). Life history can be regarded as the trade-offs made by individuals that will maximise their reproductive fitness by adapting to constraints as a consequence of selective pressures (Fisher 1958; Schaffer 1974; Hirshfield and Tinkle 1975; Boyce 1985, Parker and Maynard Smith 1990; Roff 1992, Stearns 1992). In other words, the evolution of life history traits and their plasticity to stochastic variation in demography and the environment will affect an individual’s reproductive output and even survival, thus influencing population dynamics.

Life history studies have been conducted for most animal taxa, although there are relatively few for long-lived species due to the need for many years of direct observations of behaviour, measurement of growth and energetics. The most comprehensive studies have focused on terrestrial animals (Clutton-Brock et al. 1985; Clutton-Brock et al. 1992; Festa-Bianchet et al. 1998; Gaillard et al. 2000; Coulson et al. 2001) and consequently, there are few comprehensive long-term investigations of known age long-lived animals in the marine environment (e.g. Lockyer 1981; Le Boeuf et al. 2000; Bowen et al. 2001). Of the marine vertebrates, marine mammals may be the most accessible for study as all remain tied to the air-sea interface by their need to breath. Furthermore, pinnipeds (seals) utilise the marine environment for foraging and terrestrial habitat (including ice) as a haul-out for breeding and other functions, during which time they can be easily monitored.

Most models of life history evolution contain demographic and physiological trade-offs that relate to the ‘optimal’ allocation and use of energy throughout an individual’s life (Boyce 1985; Stearns 1992) to maximise lifetime reproductive output. In most environments, resources are thought to limit growth, reproduction and maintenance; therefore, an increased allocation to one will reduce the amount available to the others (Gadgil and Bossert 1970). This process may be thought of as ‘bet hedging’ that will reduce risks and maximise lifetime reproductive success. Recently evolutionarily stable strategy (ESS) models have been widely adopted in the explanation of life histories (for example Charnov 1997; Kruuk et al. 2000). This has allowed the decisions made by

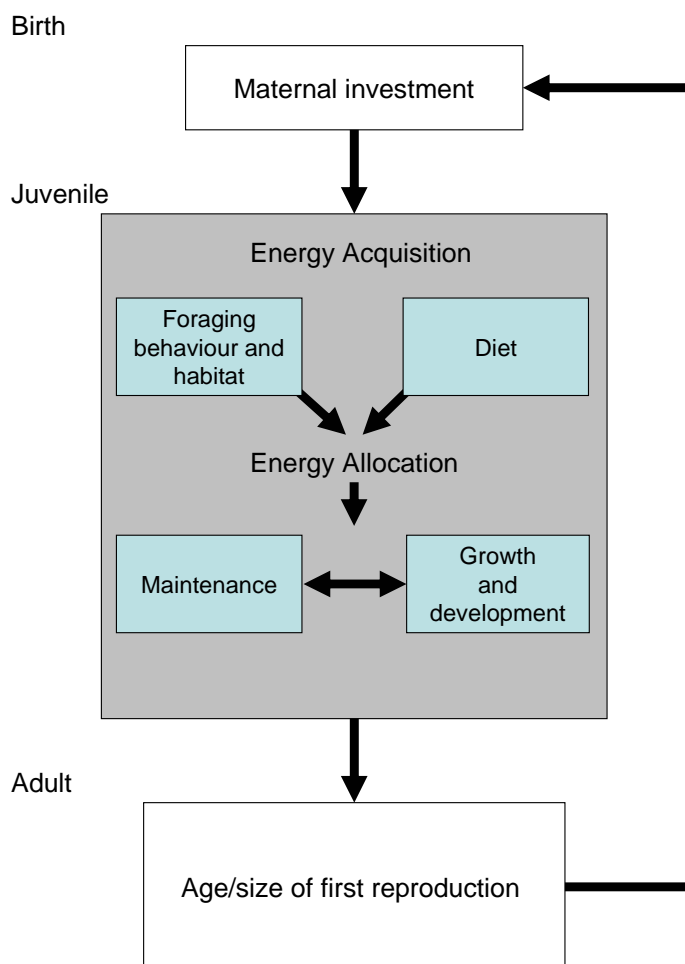
individuals to achieve maximum fitness to be examined in relation to the decisions of others (Parker and Maynard Smith 1990) and account for density-dependant effects on allocation of energy and the evolution of life histories strategies. Two important factors that influence the allocation of energy are body size and potential fecundity. These two factors underpin the trade-off of resources for growth and reproduction for instance, whether to grow faster to reach breeding age/size earlier may increase potential fecundity but will result in increased risk of mortality, though this may also confer a smaller adult size which may in turn reduce any offspring's probability of survival (Sadler 1969). An alternative strategy may be to delay maturation, allowing an increase in body size, and increasing the potential quality and survival of offspring. Furthermore, the allocation of energy will also change during different stages of an individual's life (Sibly and Calow 1983) and the flexibility in strategies optimises the energy trade-off as a consequence of the cost of reproduction (Bell 1984) and environmental variability (McNamara and Houston 1996).

Environmental variability, through intra-and inter-annual variation in both climate and the availability (and quality) of resources has been shown to influence reproductive success and early development and survival (Lack 1966; Boyce 1979; Sæther 1997) for many species (Albon et al. 1987; Orzack and Tuljapurkar 1989; Clutton-Brock et al. 1992; Hakkarainen and Korpimäki 1994; Benton et al. 1995; Henry and Ulijasek 1996; Lindström 1999; Coulson et al. 2001; Post and Parkinson 2001). Although inter-annual variation, such as 'El Niño' and 'La Niña' events, has been shown to influence productivity and have effects on population dynamics (Huber 1987; Sydeman et al. 1991) that may cause catastrophic changes and regime shifts in ecosystems (Ruhl et al. 2004; Tynan 2004), seasonality (i.e. within year variation in climate) may be a more pervasive influence on the evolution of life histories strategies (Millar 1981; Boyce 1985; Sæther 1997), especially for species that live through many seasons in a lifetime and would be subject to multiple periods of resource limitation.

### Juveniles: an important component of populations

Although behavioural development early in life is known to be important for survival and future breeding success, much of the work to date has focused on parental investment and density-dependence effects constraining populations (Clutton-Brock et al. 1992; Festa-

Bianchet et al. 1998; Albon et al. 2000; Coulson et al. 2001). Juvenile animals are defined in this study as being independently foraging individuals which are growing toward maturity, and which are no longer dependant on energy from earlier maternal investment (Fig. 1.1). Juvenile animals are an important demographic group that are often overlooked in life history studies, particularly in long-lived species (Lindström 1999), though there are exceptions (such as Packer et al. 1988; Le Boeuf 1994a). Importantly, juveniles of long-lived species may be subject to both intra- and inter-annual environmental variation before reaching maturity (Schmidt et al. 2001). Understanding these processes and their influences on juvenile development and growth will help understand and distinguish the effects of intrinsic (age, sex and state differences) and extrinsic (environmental) factors for future reproductive success, survival and population change.



*Fig. 1.1. A diagram representing the energy flow for southern elephant seals. The grey box indicates energetic trade-offs during the juvenile stage of life.*

As juveniles, individuals need to grow rapidly to maximise their lifetime reproductive fitness. This is more pronounced in polygamous species that show pronounced sexual dimorphism and where reproductive success in one sex (generally males) is highly variable (Trivers 1985; Clinton 1994). Larger body size within a species can increase both lifetime reproductive success and probability of survival of an individual and their offspring (Bryden 1969; McCann 1981; Clinton and Le Boeuf 1993; Roff 1992; Stearns 1992). Therefore, there are advantages to developing increased growth rates but may be opposed by a lower probability of survival. Furthermore, changes in weather and food availability and quality (Sæther 1997; Lindström 1999) have a direct effect on the acquisition of energy, thus affecting the allocation of energy to different functions (growth or maintenance) of entire cohorts (Rose et al. 1998). Sexual selective pressures may therefore be linked to environmental variation because this may inhibit growth rates (Coulson et al. 2001) and survival (Clutton-Brock et al. 1985; Lindström 1999). However, phenotypic plasticity in growth patterns combined with ontogenetic differences in behaviour may reduce competition for resources and the negative effects of environmental variation (Painka 1981; Polis 1984; Schoener 1986; Post and Parkinson 2001; Bolnick et al. 2003). The end result will be ontogenetic niche shifts (Woodward and Hildrew 2002), and ultimately resource partitioning of total niche width of the species attributed to the age/size structure of the population (Warren 1996; Williams and Martinez 2000; Bolnick et al. 2003). A reduction in intra-specific competition through resource partitioning has been observed for many species (Polis 1984) over a range of spatial scales, especially when resources are limited and environmental predictability is low (Perry 1996; Kato et al. 2000; Wikelski and Wrege 2000; Bowen et al. 2002; Pearson et al. 2002; Bradshaw et al. 2003). Therefore, ontogenetic shifts in morphology, habitat use and foraging behaviour may promote population stability more effectively over evolutionary time (Polis 1984).

### Elephant seals as a model species

Southern elephant seals (*Mirounga leonina*) are an excellent species for studying life history of a long-lived species within a dynamic marine ecosystem, along with their northern congener *M. angustirostris* (reviewed in Le Boeuf and Laws 1994). They are a highly dimorphic species where males at maturity are almost ten times larger than their female partners (Laws 1994) and sexual divergence occurs early in life. Although they are predominantly a marine forager, their annual life cycles are highly synchronised and

include two haul-outs each year when they are accessible for study and the deployment of tracking devices to monitor their behaviours while foraging. Also throughout this life cycle the seals are continually accumulating energy, stored as blubber, for maintenance while fasting ashore. Thus this deposition of fat could be used as an index of foraging success.

The life cycle of southern elephant seals is a combination of terrestrial haul-outs required for breeding and moulting interspersed with long periods at sea foraging, which is similar in phase to that of northern elephant seals (Clinton 1994). In the case of juveniles, the adult breeding haul-out is replaced with a mid-year haul-out (Carrick et al. 1962; Hindell and Burton 1988). This life cycle imposes different physiological constraints on individuals that change with maturity. The annual cycle of juveniles is unusual in that it incorporates a facultative mid-year time ashore (haul-out) not associated with the annual moult that occurs from November to January (Le Boeuf and Laws 1994; Kirkman et al. 2001). The purpose of this mid-year haul-out is unclear; however, the possibilities include physiological restriction, parasite reduction, social stimulation and a mechanism for reducing intra-specific competition (Carrick et al. 1962; Condry 1979; Ling and Bryden 1981; Neumann 1999, Chapter 4). With no clear function (such as moulting or breeding) it may be assumed that juveniles have relatively low metabolic costs during this time (Robbins 1993), and approximate to an on-shore metabolic maintenance baseline. This provides a valuable point of comparison for the energetic cost of maintenance during the annual moult.

Foraging success ultimately determines how much energy an individual will have to allocate to maintenance, growth and development. Elephant seals have broad foraging ranges and are generalist foragers. The foraging ecology of elephant seals has been studied extensively in terms of habitat use (Hindell et al. 1991a; McConnell et al. 1992; Slip et al. 1994; Le Boeuf 1994b; Le Boeuf et al. 1996; McConnell and Fedak 1996; Stewart 1997; Slip 1997; Jonker and Bester 1998; Le Boeuf et al. 2000; van den Hoff et al. 2002), diving behaviour (Hindell et al. 1991b; Thorson and Le Boeuf 1994; Le Boeuf et al. 1996; Hindell et al. 1999; Irvine et al. 2000; Le Boeuf et al. 2000; Hindell et al. 2000; Field et al. 2001; McConnell 2002; Buiw et al. 2003) and diet (Rodhouse et al. 1992; Green and Burton 1993; Antonelis et al. 1994; Slip 1995; Daneri et al. 2000; Daneri et al. 2002; Bradshaw et al. 2003; van den Hoff et al. 2003; van den Hoff et al. 2004). From these studies we have a

good understanding of the overall foraging ecology of elephant seals. However, most studies have been focused on adults or broad comparisons between adults and juveniles. Few have compared differences within the juvenile stage of life (Rodhouse et al. 1992; Stewart 1997; Le Boeuf et al. 2000).

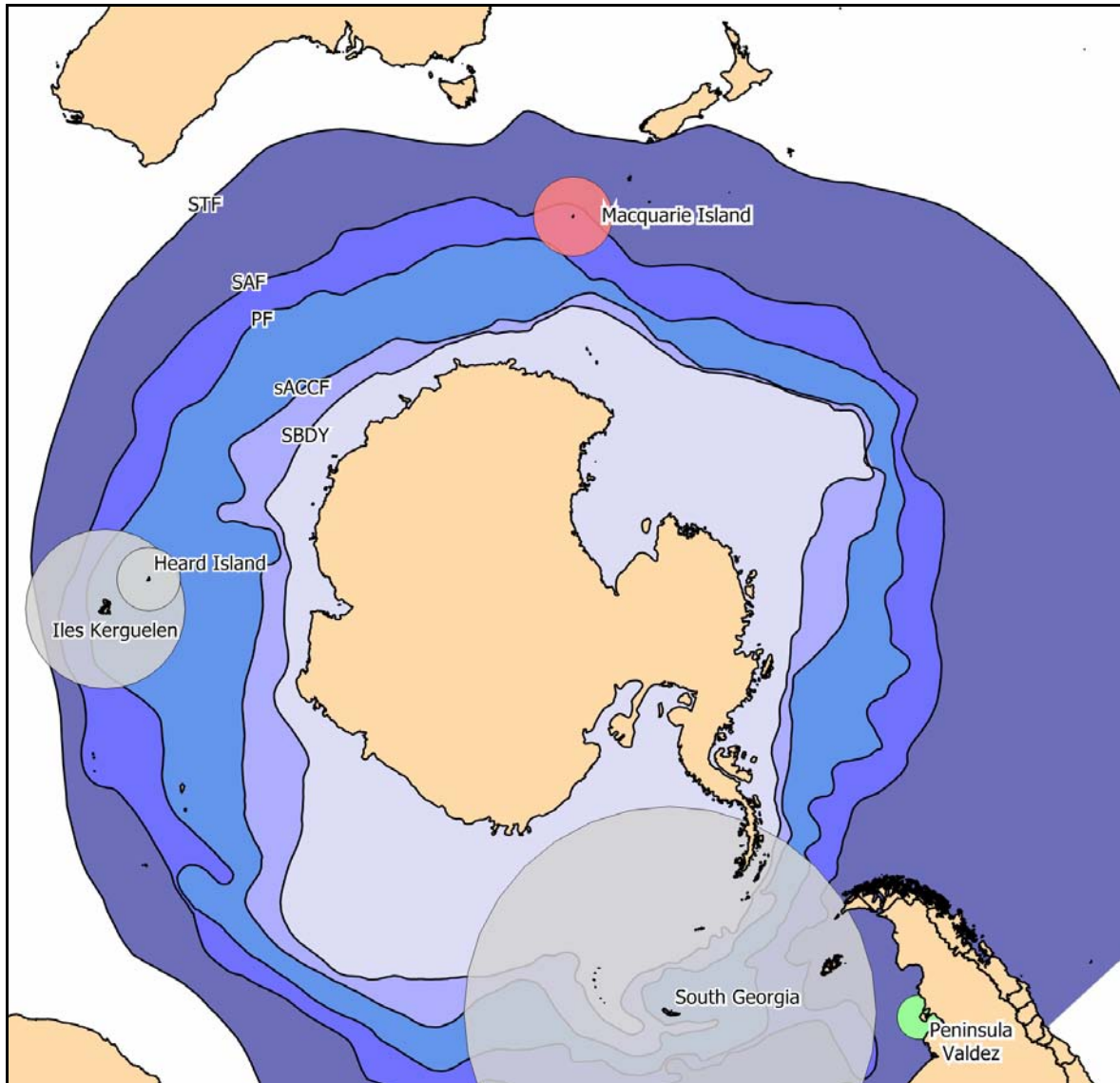
The development and growth of juveniles is affected by two factors, energy acquisition and allocation. Both of these are also influenced by intrinsic (biological) and extrinsic (environmental) factors. The intrinsic factors, age, sex and physiological differences may be regarded as adaptive processes through phenotypic variation to constraining extrinsic factors (availability and quality of food or other resources and climate changes). These combined factors influence juvenile behaviour in a complex interaction that determine how evolutionary and ecological aspects of life history strategies influence population dynamics.

### Southern elephant seals and their environment

The Southern Ocean has broad- and fine-scale structures that are defined by the physical properties of the region's different water masses (Orsi et al. 1995; Rintoul et al. 1997; Budillon and Rintoul 2003). These physical divisions provide a diversity of habitats that influence the distribution, diversity and abundance of the biological communities they support (Lutjharms 1990; Rodhouse and White 1995; Arrigo et al. 1998; Constable et al. 2003; Hosie et al. 2003). The distribution of biological resources within the Southern Ocean is highly variable, unpredictable and patchy (El-Sayed 1988; Constable et al. 2003). Though a great deal is known about the krill life cycle and populations (Nicol and Endo 1999; Nicols et al. 2000), at present little is known about other organisms in mid-trophic levels, especially the intermediate predators such as fish and squid (Rodhouse and White 1995).

Southern elephant seals, though morphologically similar, are ecologically different from their northern congener, in habitat and predation (Le Boeuf and Laws 1994) and have very different juvenile rates of survival (Le Boeuf 1994a). Southern elephant seals are major consumers of biomass, primarily squid and fish (Boyd et al. 1994; Bradshaw et al. 2003; Hindell et al. 2003b) in the Southern Ocean with a global distribution and across all physical divisions. Four main breeding populations have been identified (Slade et al. 1998;

Hoelzel et al.2001; Fig. 1.2): South Georgia (population size ~ 400, 000) in the south Atlantic, Iles Kerguelén and Heard Island (~ 220,000) in the Indian Ocean, Macquarie Island (~ 76,000) in the south Pacific Ocean, and on Peninsula Valdez (~ 42,000) in Argentina (McMahon 2003). There is estimated to be little gene flow between these populations (Slade et al. 1998; Fabiani et al. 2003).



*Fig. 1.2. The four main breeding populations of southern elephant seals. Filled circles are scaled to represent population size for populations greater than 5000 individuals and the colours represent the current population status; green - increasing population, grey – stable, and red decreasing. Also shown are the fronts of the Southern Ocean STF – sub-tropical front, SAF- sub-Antarctic front, PF – Polar Front, sACCF – sub-Antarctic circumpolar current front and the SBDY – Southern boundary of the Antarctic circumpolar front (form Orsi et al. 1995; Rintoul et al. 1997)*

The global population in recent years has increased from 664,000 in 1994 (Laws 1994) to ~ 740,000 in 2001 (McMahon 2003). The increasing population at Peninsula Valdéz has mainly driven this overall increase. The South Georgia population has remained stable over the past few decades. The population in the Indian Ocean at Iles Kerguelén and Heard Island has remained stable since 1990 after declining since the 1950s (Guinet et al. 1999; Slip and Burton 1999). However, the Macquarie Island population has continued to decrease (McMahon 2003) for reasons that are unclear (Hindell 1991). Though only a small population, the Marion Island population in the south Indian Ocean has also continued to decrease (Bester and Wilkinson 1994; Pistorius et al. 2001; Bradshaw et al. 2002) until recently (Pistorius et al. 2004). While decreasing, these two populations have been the focus of long-term demographic studies that have shown a greater rate of decrease at Marion (2.5 % per year) than at Macquarie (1.7 % per year) and identified key population parameters that influence the rates of population change (McMahon et al. 2003). The primary reason for these declines between the 1950s and 1990 has been suggested to result from food limitation with inter-island differences attributed to factors such as inter-specific competition and predation (McMahon et al. 2003).

Recent modelling of the Macquarie and Marion Island populations has indicated that age specific survival is higher at Macquarie than Marion, and females have higher overall survival rates than males (McMahon et al. 2003). Adult survival was the same at both islands, but juvenile survival (1-3 years) was reduced at Macquarie. Pistorius and Bester (2002) and Pistorius et al. (2004) concluded that juvenile survival was not an important influencing factor in population numbers, but the comparative study by McMahon et al. (2003) concluded that juvenile survival is a key parameter in influencing the rates of population change. The juveniles from Marion also showed increasing rates of survival from 1 - 4 years of age, whereas the Macquarie individuals showed higher 1<sup>st</sup>- and 2<sup>nd</sup>-year survival, but lower 3<sup>rd</sup> year survival. These data show important changes between rates of survival in second and/or third year that are as yet unexplained.

Resource limitation has been suggested as the primary reason for the change in numbers of these populations (Hindell et al. 1994; McMahon et al. 2004). This, coupled with the importance of juvenile rates of survival for population change, may provide some insight into explaining the differences between populations. For juveniles to reach breeding

capacity they must forage successfully, although this is difficult to observe directly as the seals are wide ranging and deep diving. Possible reasons for these differences in rates of survival may include changes in foraging areas, changes in foraging strategies, associated changes in prey availability, differences in the seasonal availability of prey, changes in morphology and physiology for growth, maintenance or provisioning toward adulthood, or possibly as a combination of all of these factors.

### Aims and thesis structure

The overarching aim of this thesis is to improve our understanding of the ecological interactions and evolutionary implications that influence the population dynamics of southern elephant seals at Macquarie Island. Juveniles have been identified as an important group influencing this population and therefore, understanding their ecology may enable a better understanding of the proximate causes of the population decline. This thesis contains 8 chapters. In Chapter 2, I present data and recommendations for safe anaesthesia and handling procedures. Development of these techniques was crucial for the data collection for the remaining chapters. The foraging ecology of juvenile seals is detailed in Chapters 3, 4, and 5, with detailed descriptions and analysis of the ontogenetic shifts in foraging range, spatial habitat use and diet, respectively. The growth and metabolic changes of juveniles are described in Chapters 6 and 7. In each of the chapters (3, 4, 5, 6, and 7) I highlight the influence of intrinsic and extrinsic factors on juvenile behaviour and development, which are drawn together and summarised in Chapter 8. The aims of each individual chapter are as follows:

#### *Anaesthesia and safe handling*

Chapter 2 presents data on the relationships between physiological status of southern elephant seals in terms of age, size and body condition (body shape index and blubber reserves) to assess and quantify the variation in sensitivity of individual response to anaesthesia for safer handling procedures. I also investigate whether serially captured seals alter their response to anaesthesia with cumulative captures.

#### *Foraging range*

Chapter 3 aims to (1) describe the regions of the Southern Ocean used by the different juvenile age-groups, (2) determine whether there were differences in areas or time spent

within broad oceanographic regions of the Southern Ocean relative to time of year (summer versus winter), and (3) determine how much time juveniles spend within fisheries-management zones which may be important for better management of both commercial fisheries and the Macquarie Island elephant seal population.

#### *Habitat use*

Chapter 4 quantifies the movement patterns of juvenile southern elephant seals and tests the hypotheses that as juveniles mature (1) the different age groups use different regions of the Southern Ocean and (2) individuals demonstrate fidelity to foraging areas that reinforce spatial separation. Observed patterns of foraging are discussed in light of the possible evolutionary mechanisms responsible for ontogenetic resource partitioning that may have occurred in a species demonstrating some of the greatest horizontal and vertical movements of any mammal.

#### *Diet composition*

Chapter 5 examines the diet of juvenile southern elephant seals for intra-specific and seasonal differences that may result from variation in at-sea behaviour. Furthermore, I address whether observed seasonal differences in metabolic rate within the juvenile age classes are a function of variation in prey species' abundance or whether it is variation due to physiological limitations. I hypothesise that 1) because juvenile seals grow and travel farther from Macquarie Island as they age, they also change their diet composition and size as a function of spatial variation in prey availability; 2) seasonal differences in at-sea behaviour and haul-out patterns affect prey availability and hence, diet composition, and; 3) there are sexual differences in diet selected due to the different metabolic requirements of males and females. Finally, where intra-specific differences have been found, I calculated the minimum sample required to find a difference using a novel approach that can be used for future lavaging studies.

#### *Metabolism*

Chapter 6 tests the hypothesis that, during the juvenile years, metabolic rate changes in response to differences in the way energy is stored and used as a function of growth and development, and that these patterns are also influenced by the function of the specific terrestrial haul-outs (i.e., mid-year or moult). Specifically, I examine changes in (1) rates of

mass loss, (2) changes in body composition and (3) energy use among different age groups, sexes and haul-out periods (moult and mid-year). Observed trends are discussed in terms of the proportions of lipid and protein used to derive the energy needed during a fast. I predict that due to earlier development, females will have reduced metabolic rates to those of similar-aged males that allow females to conserve energy and increase fecundity.

#### *Growth and condition*

Chapter 7 describes annual and seasonal growth in length, mass and the associated changes in body composition of southern elephant seals between the ages of one and four years. I test the hypotheses that (i) rates of gain for overall, lean and blubber masses during summer and winter change in relation to seasonal environmental variability of the Southern Ocean and, (ii) males and females diverge and have different growth strategies due to sexual dimorphism and earlier development toward age at primiparity in females.

#### *Conclusions*

Chapter 8 draws on each of the preceding chapters, synthesising biological and environmental interactions that influence the juvenile stage of their life history may be important in affecting the dynamics of the Macquarie Island southern elephant seal population.

#### *Thesis structure*

This thesis has been written as a series of papers with a number of co-authors from the Antarctic Wildlife Research Unit, the Key Centre for Tropical Wildlife Management and the Australian Antarctic Division. Other than this introductory chapter and a final summary/conclusions chapter, each chapter has been written as paper that has been submitted to or accepted for publication in peer-reviewed journals. As such, there may be some small repetition between the methods section in each chapter and focused citations due to journal requirements. While I have been the senior author for each of the papers and was responsible for organising data collection and analyses, the contribution of the co-authors was either during fieldwork, laboratory and data analysis or in the preparation of manuscripts for publication. The co-authors are listed with the title and journal reference at the start of each chapter and their contribution detailed in the statement of publication and co-authorship.

Intravenous anaesthesia of elephant seals (*Mirounga leonina*) using Tiletamine and Zolazepam: effects of age, size, condition and function of haul-out.

Published as: Field IC, Bradshaw CJA, McMahon CR, Harrington J, Burton HR (2002) Intravenous anaesthesia of elephant seals (*Mirounga leonina*) using Tiletamine and Zolazepam: effects of age, size, condition and function of haul-out. Vet Rec 151:235-240

## Introduction

Life history studies of wild pinnipeds often rely on the seals being restrained, either physically or chemically, to obtain information on diet, physiology and dive behaviour (e.g., Slip 1995; Hindell et al. 1998). The aim of any anaesthetic procedure is to provide a reliable method of immobilisation with predictable responses from the animal, rapid induction of anaesthesia, and a brief recovery time, thereby minimizing disturbance due to restraint (Haigh 1978). Many studies have documented the successful use of cyclohexamines such as tiletamine on pinnipeds (Geraci 1973; Englehart 1977; Trillmich and Weisner 1979; Shaughnessy 1991; Gales and Burton 1987a; Woods et al. 1989; Slip and Woods 1996; McMahon et al. 2000), even though this taxon remains difficult to anaesthetise (Geraci 1973; Geraci et al. 1981; Parry et al. 1981; Mitchell and Burton 1991). Pinnipeds are adapted physiologically to live in extreme environments, so sedation is often accompanied by side effects such as hypothermia and apnoea (i.e., the temporary interruption of normal breathing patterns) (Baker et al. 1988; Gales 1989; Mitchell and Burton 1991; Woods et al. 1994). However, reducing initial dose rates and administering the anaesthetic intravenously reduces the severity and frequency of such side effects (Slip and Woods 1996; McMahon et al. 2000).

Some studies have suggested that physiological status is important in sensitivity and response to anaesthetics in southern elephant seals (Gales and Burton 1987a; Woods et al. 1989; McMahon et al. 2000). Woods et al. (1989) suggested that the relationship between physiological state and sedation is complex and must be considered when preparing to anaesthetise southern elephant seals (*Mirounga leonina*) to minimize the occurrences of apnoea and other side effects.

This study presents data on the relationships between the physiological status of southern elephant seals in terms of age, size and body condition (body shape index and blubber reserves) to assess and quantify the variation in sensitivity of individual response to anaesthesia. I also investigate whether serially captured seals alter their response to anaesthesia with cumulative captures.

## Methods

Between November 1999 and February 2001, 1033 southern elephant seals were anaesthetised intravenously (after McMahon et al. (2000)) as part of a long-term demographic study of a declining population on Macquarie Island (Hindell et al. 1994). Immobilisation was required for safe handling while body condition was assessed. Some individuals were fitted with archival tags for at-sea behavioural studies (Slip et al. 1994; Irvine et al. 2000; Hindell et al. 2000), stomach-lavaged for the assessment of diet composition (Green and Burton 1993; Slip 1995), and biopsy-sampled for blubber composition (Iverson et al. 1997). Seals ranged in age from 15 months to seven years at the time of capture over six different phases of their life cycle. Typically, seals were caught and immobilised as they returned for breeding, moulting and mid-year haul-outs after foraging trips. Some seals were also caught at the end of these haul-outs before returning to sea.

Seals were caught by hand using a canvas bag placed over the head and injected intravenously, via the lower lumbar region of the extradural vein, with a combined 1:1 mixture of tiletamine and zolazepam (Telazol<sup>®</sup>, Forte Dodge, Castle Hill, NSW, Australia) (McMahon et al. 2000). The capture technique is discussed in detail by McMahon et al. (2000). The combined dose rates of tiletamine and zolazepam varied between 0.3 to 0.7 mg kg<sup>-1</sup> depending on the level and duration of anaesthesia required. Initial doses were given after body mass was estimated on the basis of previous experience by field personnel. Subsequent to sedation, each individual was weighed to the nearest kg (see below), thus exact dose rates (e.g., mg of drug injected per kg of seal) could be calculated. Restraint and disturbance to seals was kept to a minimum. Drug induction and recovery times were recorded for all seals. Any periods of apnoea were noted. Induction time was defined as the time from injection of the anaesthetic until the seal failed to respond to head patting and ceased struggling (McMahon et al. 2000). The recovery time was defined as the time from sedation until the seal could raise its head and maintain it in the elevated position (Woods et al. 1994). For this study, a seal was considered apnoeic when it had stopped breathing for longer than five minutes (Slip and Woods 1996). Breathing and capillary refill of the gums were monitored constantly (Woods et al. 1994). An endotracheal tube, oxygen, and the respiratory stimulant, Doxapram, were available in the event of prolonged apnoea or poor capillary refill, but were never required.

Once anaesthetised, the seals were weighed ( $\pm 1$  kg) and measured ( $\pm 10$  mm). Body weight and morphometric measurements were made to calculate indices of body shape and volume (Fig. 2.1). Relative measures of blubber thickness were obtained using an ultrasound backfat depth system (A-Scan Plus<sup>TM</sup>, Sis-Pro Inc., Woodbury, MN, USA). Total seal volume (TSV) was calculated by modifying the method of Gales and Burton (1987b). This method assumed that individuals were circular in cross section, such that the diameter for any cross-section was equivalent to the side height. It was assumed that all the blubber lies in the hypodermis and over the whole body and that the flippers contain insignificant amounts of subcutaneous fat (Bryden 1967). Measurements were divided across seven sections (Fig. 2.1), with the head and hips to the base of the tail forming cones and the rest of the body sections forming truncated cones. The girth measurements ( $G$ ) were used as basal circumferences in the calculation of full and truncated cones ( $C$ ).  $G_1$  and  $G_6$  were used for the circumferences of the head and hips to the end of the tail cones ( $C_1$  and  $C_7$ , respectively). The height ( $K$ ) of these cones was calculated by subtracting the  $G_1$ - $G_6$  measurement from the standard length and then halving this value. For the rest of the body sections, it was assumed that these form truncated cones. Here, the larger of the girths formed the base of the cone, and the height ( $H$ ) of the cone was either a)  $H_a$  = half the distance between  $G_1$  and  $G_3$  for the anterior cones  $C_2$  and  $C_3$ , or b)  $H_p$  = one third the distance between  $G_3$  and  $G_6$  for the posterior cones  $C_4$ ,  $C_5$  and  $C_6$ . Therefore, the volume of the anterior section of the seal was:

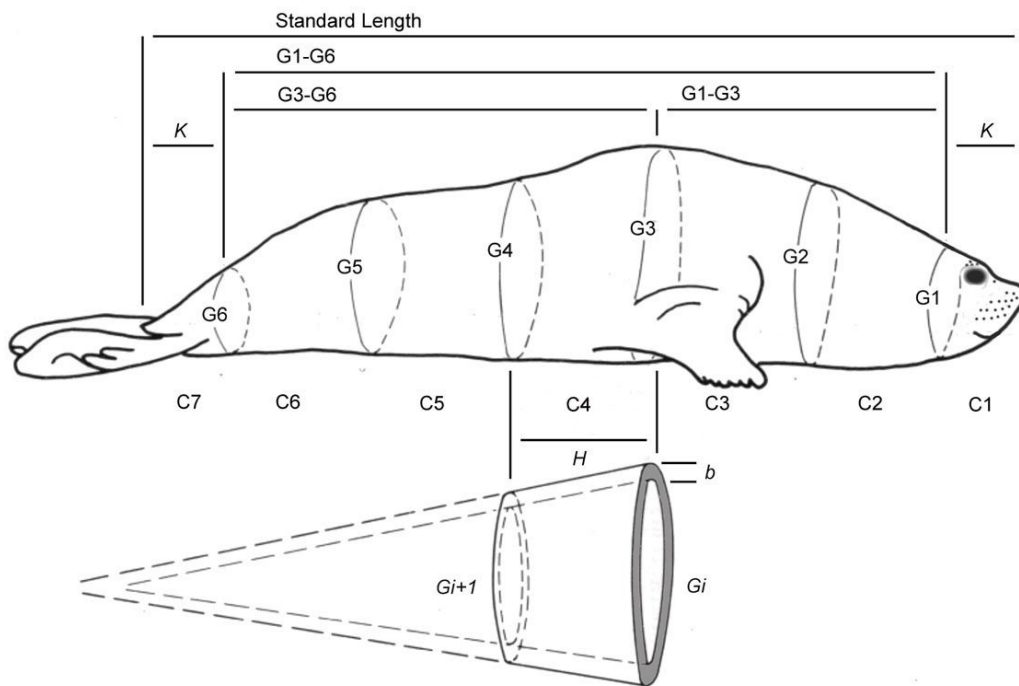
$$V_{anterior} = \sum_{i=2}^3 \left( \frac{\pi H_a}{3} \left( \left( \frac{G_i}{2\pi} \right)^2 + \left( \frac{G_i G_{i+1}}{\pi^2} \right) + \left( \frac{G_{i+1}}{2\pi} \right)^2 \right) \right) + \frac{\pi K}{3} \left( \frac{G_1}{2\pi} \right)^2$$

Where  $G_i$  = girth at base of cone and  $G_{i-1}$  = girth at the top of the cone. The volume of the posterior section was then:

$$V_{posterior} = \sum_{i=3}^6 \left( \frac{\pi H_p}{3} \left( \left( \frac{G_i}{2\pi} \right)^2 + \left( \frac{G_i G_{i+1}}{\pi^2} \right) + \left( \frac{G_{i+1}}{2\pi} \right)^2 \right) \right) + \frac{\pi K}{3} \left( \frac{G_7}{2\pi} \right)^2$$

The volumes of both sections were summed ( $V_{anterior} + V_{posterior}$ ) to calculate TSV. Blubber thickness ( $b$ ) was measured at each of the girth sites along the seal's dorsal side (Gales and

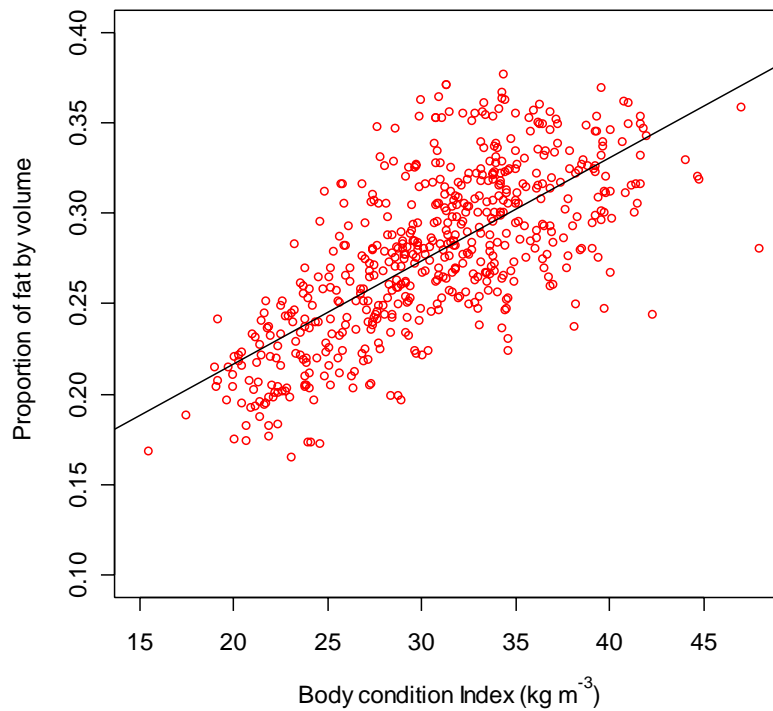
Burton 1987b; Slip et al. 1992). The blubber depth was subtracted from the radii of the cones to calculate the volume of the inner cone (Fig. 2.1). Here I assumed that blubber thickness was constant around the seals' girth. The total volume of these cones was calculated by the same method as for the TSV, and was assumed to represent the total volume of lean tissue (TLV). The total blubber volume (TBV) was calculated by subtracting TLV from TSV.



*Fig. 2.1. Morphometric measurements used in the calculation of a blubber volume. G1 to G6 represent the circumference of the body at sites 1 to 6, thus creating 7 cones (5 truncated and 2 terminal cones). The depth of blubber ( $b$ ) was assessed at the dorsal surface of all 6 sites and used to calculate total blubber volume (TBV).*

Body condition was assessed using two methods. Firstly, I calculated the proportion of blubber by volume (BV) as  $TBV/TSV$ . However, BV could only be calculated for a subsample of the data ( $n = 553$ ) since these were the animals for which six dorsal blubber thickness measurements were taken. The remaining animals could not be assessed for BV since these measurements were not taken due to either remoteness of capture or malfunction of the ultrasound equipment. Therefore, for these remaining animals an index of body shape was used as a surrogate index of condition (where condition index (CI) =  $\text{body mass} / \text{standard length}^3$  - Virgl and Messier 1993; Chabot 1994). Although BV was

considered a superior measurement of body condition, CI was found to be a reasonable proxy index of blubber content (Fig. 2.2;  $r^2 = 0.493$ ,  $F_{1,553} = 539.9$ ,  $P < 0.001$ ). Thus, for those analyses where the numbers of animals with BV estimates were low, I also included a second analysis composed of the larger sample of animals with the estimate of CI.



*Fig. 2.2. The positive relationship between proportion of blubber by volume (BV) and body condition index (CI) ( $r^2 = 0.493$ ,  $F_{1,553} = 539.9$ ,  $P < 0.001$ ).*

Induction times and recovery times were analysed in relation to dose rate, sex, age and condition. Recovery times and recovery rates (see below) were  $\log_e$ -transformed to normalise the data and to homogenise variances among factor levels (Sokal and Rohlf 1981). These transformed variables were used for all subsequent analyses. Mass-specific dose rate explained  $> 50\%$  of the variation in recovery time ( $r^2 = 0.502$ ,  $F_{1,1031} = 1041.7$ ,  $P < 0.001$ ; Fig. 2.3), so for all subsequent analyses, recovery times were weighted by the reciprocal of dose rate to control to control for level of anaesthesia required and mass of the seal. Henceforth, 'recovery rate' refers to the weighted measure of recovery time. Age was calculated as the age of the seal to the nearest month at the time of capture.

To test for sex differences in blubber volume, I combined animals aged 1 to 4 years (i.e., those ages for which I collected data on both males and females) and ran a one-way, unbalanced, general factorial general linear model (GLM) in SPSS (for Windows version 7.5.1) of the form:

$$\text{proportion blubber by volume} = \text{sex} + \text{error}$$

where the *sex* term was designated as a random term due to the random sampling of known age seals as they hauled-out, and the *error* term represents unexplained variation in the response variable, proportion of blubber by volume.

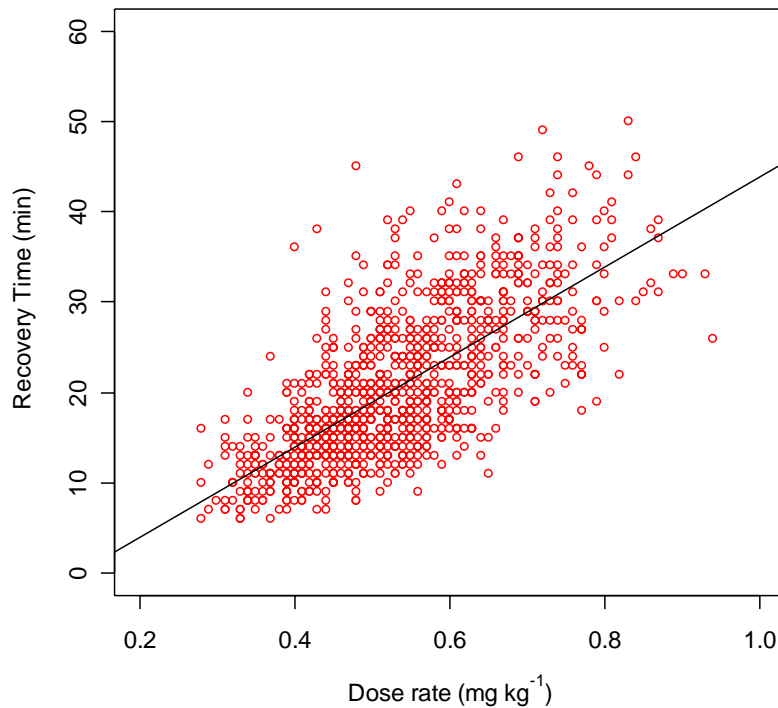


Fig. 2.3. The positive relationship between mass specific dose rates and recovery time ( $r^2 = 0.502$ ,  $F_{1,1031} = 1041.7$ ,  $P < 0.001$ ).

Unbalanced, general factorial GLMs were employed to describe the relationships between age, sex and condition to times of induction and to the recovery rates. Models tested the effect of all main factors (e.g., age, sex and condition) and their two- and three-way interactions on the response variables, induction time and recovery rate. For example, the saturated model is:

$$\log_e(\text{response}) = \text{age} + \text{sex} + \text{cond} + \text{age} * \text{sex} + \text{age} * \text{cond} + \text{sex} * \text{cond} + \text{age} * \text{sex} * \text{cond} + \text{error}$$

and all models considered included all combinations of terms presented in the saturated model. Here, *age* and *sex* were designated as a fixed terms and *cond* (condition) as a covariate. A '\*' between factors indicates an interaction term.

There was no *a priori* reason to assume a single model to describe the contribution of terms and their interactions to the response variables, so I used a form of model selection with Akaike's Information Criteria (AIC) to select the most parsimonious model (Lebreton et al. 1992). AIC is calculated as:

$$AIC = 2LL + 2p$$

where  $LL = -2 \log\text{-likelihood}$  calculated from the mean squared error (MSE) and the Type III sum of squares error (SSE) for each general factorial GLM, and  $p$  = the number of model parameters. AIC values are then ranked on a relative scale from 0 (poor) to 1 (good) (i.e., model weight). Thus, 'best-fit' model(s) have the lowest AIC value and the highest model weight (Lebreton et al. 1992).

Furthermore, I used a repeated-measures GLM to test for within-individual response to the model terms. In these analyses, only CI was used as a measure of condition because of the reduced sample size for animals for which the index of BV was calculated (only 555 animals were assessed for blubber depth). All means are reported with  $\pm$  one standard error (SE).

Differences in recovery rates among haul-out seasons (i.e., start of breeding, start of moult and start of mid-year) were tested using a GLM of the form:

$$\log_e(\text{recovery rate}) = \text{haul-out period} + \text{error}$$

where *haul-out period* was designated as a random class term.

I also examined the relationship between the numbers of captures experienced by a seal during the course of the study to the recovery time at the final capture. These seals were seals of all ages that had been caught multiple times. Few animals were caught  $> 5$  times (see Results); therefore, I used a Monte Carlo randomisation (Manly, 1997) to examine the relationship between recovery rate and number of previous captures ( $n = 211$  animals with  $> 1$  capture). This method involves randomising the order of recovery rates relative to capture rates 10,000 times and assessing the squared difference between recovery rate and number of captures per individual. For each iteration, the sum of the squared difference ( $SS_{\text{rand}}$ ) between these values was compared to the sum derived from the true order ( $SS_{\text{true}}$ ). The number of times  $SS_{\text{rand}}$  was less than  $SS_{\text{true}}$  in the 10,000 iterations gave the probability ( $P_{10,000}$ ) that the relationship, if any, was due to chance. This method was employed because of the heterogeneity of variances among levels of the capture factor (i.e., number of times captured). Examination of the data indicated that a  $\log_e$ -transformation was incapable of homogenising variances or normalising recovery rates. Thus, the distribution-free randomisation approach to examine the effects of cumulative anaesthesia provided results that did not violate parametric modelling assumptions (Manly, 1997).

## Results

The mean dose rate was  $0.533 \pm 0.003$  mg/kg, resulting in mean induction and duration times of  $36.5 \pm 0.4$  seconds and  $20.6 \pm 0.3$  minutes ( $n = 1033$ ) respectively. There were no fatalities or periods of apnoea and all seals were resighted at Macquarie Island subsequent to anaesthetic procedures. None of the adult females caught during the breeding season deserted their pup upon recovery from anaesthesia.

On average, female seals had a greater proportion of blubber than males for the ages of 1 to 4 years ( $F_{1,329} = 16.18$ ;  $P < 0.001$ ) (Fig. 2.4). For both CI and BV, there were significant changes in body condition between the start of haul-out and those measured at the end (Table 2.1).

### *Induction times*

AIC model selection failed to detect a single, best-fit model for induction times, nor did any models explain a significant amount of variation in induction time. Thus, there were no detectable effects of sex, age or condition (Fig. 2.5) on induction times (Table 2.2).

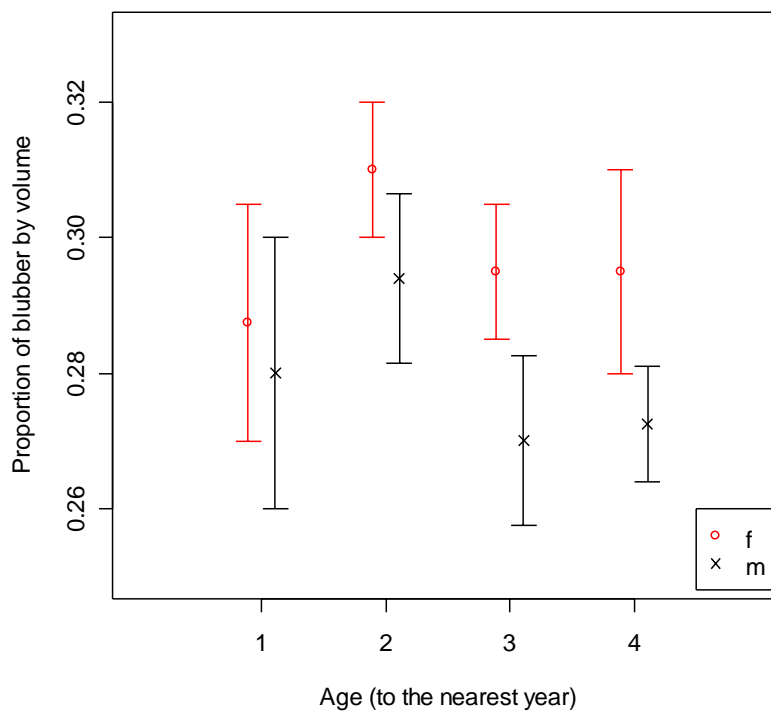
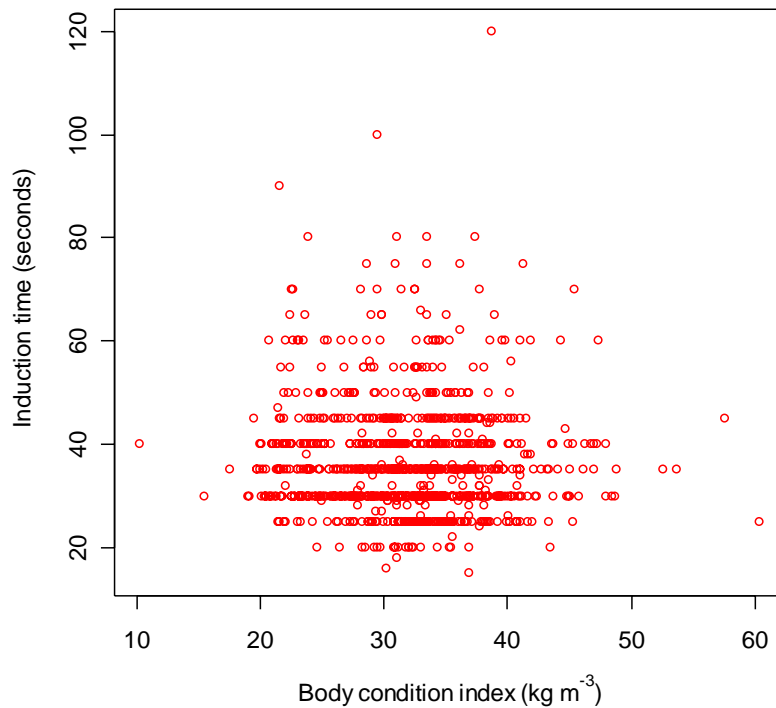


Fig. 2.4. The proportion of blubber by volume (BV) for male and female seals between 1 and 4 years of age.

Table 2.1. The mean values for the different condition measures with age and at the start and end of haul-outs (where BV is the proportion of blubber by volume and CI is an index of body shape was = body mass / standard length<sup>3</sup>).

Age (yrs)	BV				CI			
	Start of haul-out		End of haul-out		Start of haul-out		End of haul-out	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1	0.318	0.005	0.227	0.006	36.075	0.303	29.832	0.806
2	0.321	0.003	0.252	0.007	35.053	0.404	26.686	0.554
3	0.303	0.003	0.242	0.006	32.901	0.269	25.512	0.495
4	0.283	0.003	0.256	0.011	32.244	0.525	25.263	1.029
5	0.273	0.011	-	-	30.872	0.529	24.301	0.605
6	0.261	0.002	0.224	0.005	30.694	0.474	22.325	0.808
7	0.276	0.003	0.218	0.004	30.992	0.566	22.648	0.371



*Fig. 2.5. Induction time expressed as a function of body condition index. No relationship was evident.*

*Table 2.2. The mean induction times (secs) for different age groups at the start and end of haul-outs.*

Age (yrs)	Start of haul-out		End of haul-out	
	Mean	SE	Mean	SE
1	35.7	0.7	38.1	1.5
2	35.5	0.8	37.8	1.2
3	34.5	0.8	36.4	1.0
4	35.5	1.0	38.9	1.9
5	36.8	2.2	36.0	6.3
6	39.8	1.2	39.5	2.7
7	41.3	1.7	45.0	2.7

### *Recovery times*

Using the condition index (CI), AIC model selection failed to detect a single, best-fit model. However, the model including CI alone had the highest AIC weight (0.1369). The model showed a weak, but significantly negative effect of condition ( $F_{1,1031} = 48.6$ ,  $P < 0.001$ ), and accounted for 4.4 % of the variation in recovery time. This model showed that seals in lower condition had longer recovery times. The next best model was for age and

CI (AIC weight = 0.1214) and showed a slight, but significantly positive influence of age (model  $r^2 = 0.052$ ; age term:  $F_{1,1030} = 10.0$ ,  $P < 0.002$ ).

Using BV, the most parsimonious model included BV alone (AIC weight = 0.1381). Here, there was a small, negative effect on recovery times ( $r^2 = 0.007$ ;  $F_{1,447} = 3.93$ ;  $P = 0.048$ ). The next best model using BV was for sex only (AIC weight = 0.1290), but this effect can be described adequately by the difference in proportions of blubber between the sexes (Fig. 2.4).

The most parsimonious models for both condition measures failed to identify an effect of sex on recovery time. For all indices of body condition there was a weak, but significantly negative effect of condition such that seals in poorer condition had longer durations of anaesthesia. There was also a slight positive age effect with older animals taking longer to recover using the model containing the age and CI terms. There was no effect of the time of year (haul-out period) on recovery time that could not be explained by differences in body condition.

Repeated measures GLM was used on individual seals caught at the start and again at the end of a haul-out period (Table 2.3) to test more explicitly the effects of sex, age and condition on recovery times by removing individual variation. Within-individual analysis demonstrated a weak, but significant effect of body condition ( $F_{1,140} = 7.9$ ,  $P < 0.008$ ), but no effect of age ( $F_{1,140} = 1.7$ ,  $P > 0.194$ ). However, when the differences in condition among individuals were considered the effect of condition was lost ( $F_{1,140} = 0.7$ ,  $P > 0.405$ ) and the effect of age became significant ( $F_{1,140} = 5.1$ ,  $P < 0.026$ ).

#### *Differences between start of haul-outs for different age groups*

There were significant differences among the start of haul-out periods in recovery rate (Fig. 2.6;  $F_{2,788} = 12.74$ ,  $P < 0.001$ ). Here, seals caught at the start of the annual moult had quicker recovery rates than during the breeding or mid-year haul-outs. However, since only adult females were present during the breeding season and recovery rate varies with age, I re-examined this relationship for adult females (comparing breeding and moult haul-outs) and for juvenile (i.e., age < 5 years) seals separately (comparing moult and mid-year haul-outs). There was no difference in the recovery rate of adult females between the start of the

breeding and moult-haul-outs ( $F_{1,117} = 0.213$ ,  $P = 0.645$ ). However, juvenile seals caught at the beginning of the moult still had quicker recovery times ( $F_{1,647} = 32.27$ ,  $P < 0.001$ ), even though they were in poor condition than those caught at the start of the mid-year haul-out ( $F_{2,647} = 6.52$ ,  $P = 0.011$ ).

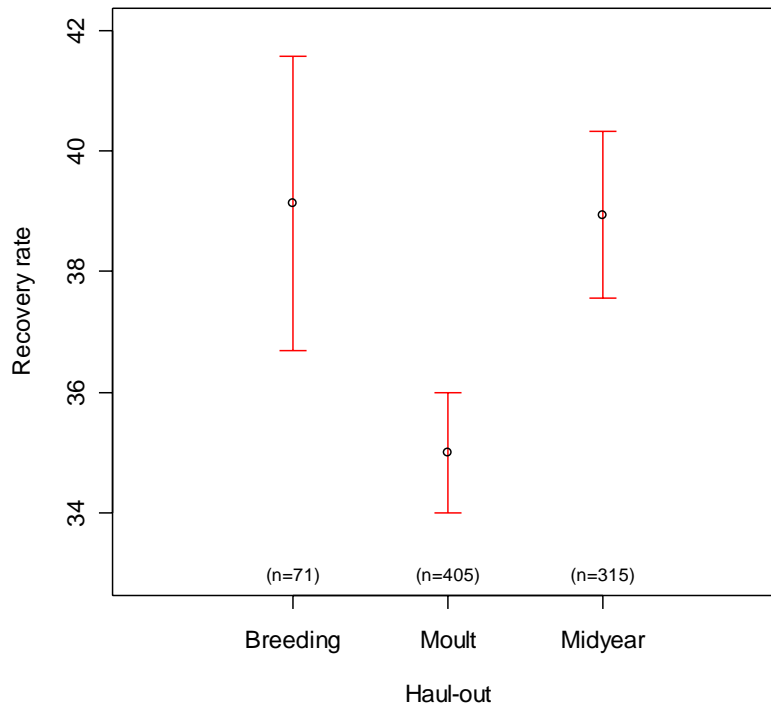


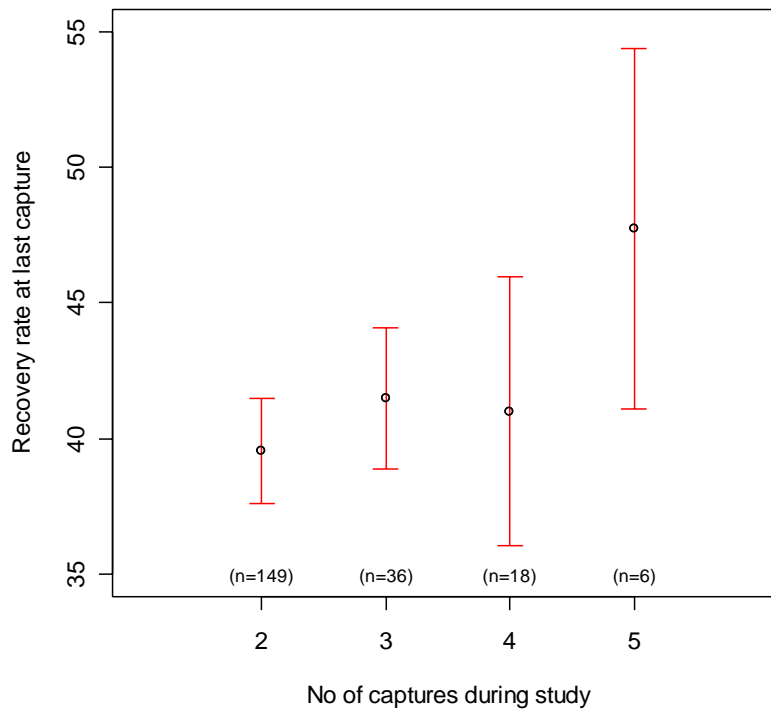
Fig. 2.6. Recovery rate ( $\bar{X} \pm 2SE$ ) relative to the start of each different haul-out period.

Table 2.3. Mean recovery times (min) for different age groups and start and end of haul-outs.

Age (yrs)	Recovery Time				Recovery Rate			
	Start of haul-out		End of haul-out		Start of haul-out		End of haul-out	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1	16.0	0.4	23.5	1.1	33.3	0.6	39.3	1.3
2	20.1	0.6	28.1	1.0	36.7	0.8	42.0	1.2
3	20.0	0.6	26.3	0.9	39.2	1.0	45.1	1.4
4	21.3	0.9	18.2	1.3	40.8	1.3	35.4	2.8
5	15.2	0.5	16.0	1.1	33.3	1.2	31.0	4.6
6	22.3	1.0	21.2	1.7	42.3	1.7	31.0	2.2
7	22.5	1.0	31.7	1.5	41.3	1.4	45.8	1.7

### *Number of previous captures*

There was a significant, albeit slight, increase in the recovery rates with the number of times an individual was caught and immobilised (Fig. 2.7). The Monte Carlo randomisation revealed a significant positive relationship ( $P_{10,000} = 0.0206$ ).



*Fig. 2.7. Recovery rate ( $\bar{X} \pm 2SE$ ) relative to the number of captures experienced during the study period.*

## Discussion

Past studies have shown that (1) the size (body mass) of a seal is the most important consideration when planning anaesthesia, and (2) use of mass-specific doses has enabled safe and reliable procedures for the capture and handling of elephant seals (Baker et al. 1988; Gales 1989; Woods et al. 1989; Wood et al. 1994; Slip and Woods 1996; McMahon et al. 2000). Many authors have described intraspecific and individual variation during anaesthesia, the reasons for which are still poorly understood. Such undescribed variation may carry an increased likelihood of risk and side effects. The method of drug administration accounts for most of the variation observed during anaesthesia. Slip and Woods (1996) showed that variation can be reduced by administering drugs intravenously

as opposed to intramuscularly. The intravenous administration of tiletamine and zolazepam resulted in rapid induction, a shorter duration of sedation and smaller required doses. This avoids many of the potential problems associated with sedation of pinnipeds, such as apnoea, hypothermia and fatality due to anaesthesia (Slip and Woods 1996; McMahon et al. 2000).

Induction times were unaffected by body condition, most likely due to the rapid uptake of anaesthetic by the system when injecting intravenously. A single bolus of anaesthetic is injected directly into the venous system and is transported rapidly to the brain, so the concentration required to invoke sedation is reached quickly (Woods et al. 1999). Since the drugs are administered directly into the blood system there is little opportunity for drug redistribution to the muscles and blubber, so no effects of body composition are expected.

McMahon et al. (2000) showed that dose rate was related positively to the recovery time ( $r^2 = 0.245$ ). However, little has been done to explain the intraspecific and individual variation in response to anaesthesia. Only a few authors have suggested some reasons for such variation (Trillmich 1979; Loughlin and Spraker 1989; Woods et al. 1989), but all have ascribed some of the variation to the physiological demands associated with breeding, moulting, absorption rates of the anaesthetic agent, and level of activity before anaesthesia. The only study to test a measure of condition is McMahon et al. (2000), which found a weak but negative relationship between condition and duration. I analysed this relationship with a greater range in age, condition and dose rates (and hence, greater statistical power) among individuals captured, thereby confirming the conclusions of McMahon et al. (2000). For the repeated-measures models, the differences in results for within- and between-individual responses to anaesthesia is to be expected because: (1) all seals are losing blubber during the course of a haul-out period, and (2) the rate of blubber loss appears to vary with age. In addition, I have demonstrated that although such a relationship exists, even precisely measured indices of body condition still account for only a small proportion of the variation in the properties of pinniped anaesthesia. The majority of the variation (after accounting for dose rates), still results from intraspecific differences that are as yet unquantified.

Intravenous injection of drugs results in a quicker distribution of the drug to the brain and liver than intramuscular injection. Therefore, recovery times were quicker (Rowland and Tozer 1995a). Tiletamine and zolazepam are lipophilic, so they accumulate more rapidly in fatty than lean tissue (Rowland and Tozer 1995b). When the drug is re-distributed, a proportion is absorbed into the fatty tissue. Hence, fatter seals are expected to have less free-drug available to prolong anaesthesia and so have shorter recovery times. I applied this knowledge to lower dose rates further and predict the seals' responses to mass-specific dose rates.

Two studies in the past associated physiological 'stresses' during the breeding season to longer durations (Trillmich 1979; Woods et al. 1989). Assuming this to be true I would expect to see differences in anaesthesia responses at different times of the year such as between breeding and moulting. I found no such differences in durations between post-partum and pre-moult females. However, I found evidence to suggest that the type of haul-out (moulting versus the midyear) had an effect on the recovery rates for juvenile seals, despite the fact that juvenile seals were, on average, fatter during the mid-year haul-out. This effect was most likely due to the difference in metabolic rates of the juvenile seals who may have a lower metabolic rate during the mid year haul-out than during the moult.

Older seals remained anaesthetised longer than younger seals for the same relative concentration of drug administered. A possible explanation may be that as seals mature, the ratio of blubber to body mass decreases, as does their metabolism (Boily and Lavigne 1997), resulting in slower metabolism of the anaesthetic agent. For pinnipeds in general, metabolic rates decrease as the juvenile approaches breeding age. It is thought that this coincides with the increase in dive depth and fasting ability while ashore for breeding and moulting (Kooyman 1985; Guppy et al. 1986; Hochachka and Guppy 1987; Hindell et al. 1991; Boily 1996; Boily and Lavigne 1997). Another alternative is that clearance rates of the benzo-cyclohexamines by hepatic metabolism decreases with age, as has been shown in humans (Rowland and Tozer 1995a). This hepatic metabolism may also be depressed by lower enzyme production in the liver, leaving more free-drug to affect anaesthesia. However, this phenomenon has yet to be tested quantitatively in non-human animals.

I found a positive relationship between the numbers of captures and recovery times; however, these results must be treated cautiously because this result is based on very few data for animals caught more than four times. However it should also be noted that, though the multiply caught seals were of all ages, there was a tendency for the animals caught more than five times to be older and therefore may have elevated recovery times due to an age effect. Nonetheless, two plausible explanations for this observation include: 1) serially captured animals were habituating to restraint, thereby entering the period of sedation in state of reduced stress. With possibly lower heart-rate entering sedation, the vascular distribution of the drugs may have been slowed relative to animals in higher states of stress at time of capture. 2) Seals caught more often may not have been as efficient in the metabolic breakdown of the drug residual as pathways used in the metabolism of the drugs are affected. This has been described for the use of diazepam (Valium<sup>®</sup>, Roche Products, Pty Ltd, Sydney, Australia) on cats (Levy et al. 1994; Center et al. 1996).

The use of simple inhalation anaesthesia has been used as an effective alternative to the injection method of anaesthesia in some phocid species (Kusagaya and Sato 2001); however, intravenous anaesthesia still has advantages over this new method. The practicalities of elephant seal handling for weighing and measuring would not allow for multiple administrations over short intervals (e.g., approximately every 2 minutes – Kusagaya and Sato 2001) to attain the durations of anaesthesia required.

Our study has linked condition and age to the duration times of elephant seal anaesthesia. Mass-specific doses of tiletamine and zolazepam injected intravenously, along with information on age and body condition of a seal, have enabled us to reduce dose rates further and to tailor the desired level and duration of immobilisation. Using this method, the risk of apnoea and other side effects associated with anaesthesia in large, wild seals is virtually eliminated.

## Summary

Southern elephant seals (*Mirounga leonina*) were caught as part of a long-term demographic study at Macquarie Island. Over 18 months, 1033 seals were caught by hand and anaesthetised intravenously with a combined 1:1 mixture of tiletamine and zolazepam (commercially available as Telazol<sup>®</sup>). I assessed the effects of variation in body condition

and age at capture of 1033 separate captures on the characteristics of anaesthesia, including induction time and dose-specific recovery rate. The size and condition of the seals were assessed using morphometric and ultrasound measurements. Recovery rates increased as body condition and age decreased, but there were no residual effects of sex. There were no fatalities or periods of apnoea greater than five minutes recorded during this study. There was a significant increase in recovery rate with the number of subsequent captures in individual seals. I suggest two explanations for such an effect: 1) Reduced stress associated with habituation to capture may reduce heart rates and vascular distribution of the drugs, or 2) drug catabolism may be less efficient with number of captures. With information on age, weight estimates and body condition, the anaesthetic procedure described here increases the control over immobilisation level and duration, and reduces handling times for wild pinnipeds.

Seasonal use of oceanographic and fisheries management zones by juvenile southern elephant seals (*Mirounga leonina*) from Macquarie Island.

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### Introduction

The Southern Ocean is a dynamic, highly variable environment with an unpredictable and patchy distribution of biological resources (El-Sayed 1988; Constable et al. 2003). The Southern Ocean has been the focus of many studies (Orsi et al. 1995; Rintoul et al. 1997; Budillon and Rintoul 2003) that have identified broad- and fine-scale structure according to the physical properties of the region's different water masses. These physical divisions provide a diversity of habitats that influence the distribution, diversity and abundance of the ecological communities (Lutjharms 1990; Rodhouse and White 1995; Arrigo et al. 1998; Constable et al. 2003).

Living resources in the Southern Ocean are managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) under article IX of the Antarctic Treaty system. The CCAMLR was designed to safeguard the marine environment, to protect the integrity of the ecosystem of the seas surrounding Antarctica and to allow the exploitation of resources within (Agnew 1997). As part of the management framework, the CCAMLR Environmental Monitoring Program (CEMP) was initiated in 1985 to relate indices of predator status and breeding success to krill availability, and to distinguish these relationships from those resulting from harvesting or natural changes (Agnew 1997). The aim of the program was chosen to focus on krill before over-fishing could have serious consequences (Nicol 1991). However, this focussed approach has meant that CCAMLR has devoted less attention to the open-ocean pelagic system. Although commercial fishing pressure has recently increased within this system, several regions have still had little fishing and present an opportunity to distinguish variation in biological and physical parameters (e.g., climate change- Viet et al. 1996; Barbraud and Weimerskirsh 2001; Weimerskirsh et al. 2003) from that due to harvesting.

Top predators have been proposed as indicators of the status of components of lower-trophic levels (Furness et al. 1993; Kerry et al. 1997; Croxall et al. 1999; Barbraud and Weimerskirsh 2001). This approach has been adopted by CEMP in an attempt to understand and model the krill-based system (Agnew 1997; Croxall et al. 1999; Hindell et al. 2003a). In the open-ocean pelagic system, one possible indicator predator that is easily accessible and has a circumpolar distribution is the southern elephant seal (*Mirounga leonina*). This species is a wide-ranging, deep-diving predator that spends more than 80 %

of its annual cycle at sea. They are major consumers of second-order producers, primarily squid and fish (Bradshaw et al. 2003; Hindell et al. 2003b). Further, it has been suggested that this species is susceptible to changes in the availability of prey (Hindell et al. 1994; Guinet et al. 1999; Slip and Burton 1999; McMahon et al. 2003), which is reflected in the status of the different populations (McMahon 2003).

A recent demographic study has shown that the survival of juveniles (aged 1-4 years) is the most important factor influencing the rate of change of elephant seal populations (McMahon et al. 2003) at Macquarie Island. As they progress from juvenile to adult foraging patterns, juveniles may be influenced by ontogenetic changes in morphology, diving behaviour, foraging areas of the Southern Ocean, the availability of prey or a combination of these factors (Hindell et al. 1994) and, therefore, may be more sensitive than adults to variation in their environment.

Although there have been several studies of foraging ecology of southern elephant seals from Macquarie Island (Slip et al. 1994; Hindell et al. 1991a; Hindell et al. 1991b; Hindell et al. 1999; Irvine et al. 2000; Field et al. 2001; van den Hoff et al. 2002; McConnell et al. 2002; Hindell et al. 2003b), most have concentrated on the adult population or naïve, recently weaned pups. Only one study has described the at-sea movements of juvenile seals (van den Hoff et al. 2002), and this was limited to seals less than 18 months old. It is therefore important to examine the foraging ecology of juvenile seals, especially given that juveniles within the Macquarie Island population constitute almost half the total population (McMahon 2003).

In this study I specifically aimed to (1) describe the regions of the Southern Ocean used by the different juvenile age-groups, (2) determine whether there were differences in areas or time spent within broad oceanographic regions of the Southern Ocean relative to time of year (summer versus winter), and (3) determine how much time the seals spent within fisheries-management zones.

## Methods

The southern elephant seal population at Macquarie Island (158° 57'E, 54° 30'S) has been the focus of a long-term demographic study since 1993 (McMahon et al. 2003).

Approximately 2000 pups were marked each year (using plastic flipper tags and hot-iron branding; McMahon et al. 1997) from 1993 to 2000. For the present study, juvenile seals were regarded as those between one- and four-years old that had not bred before (McMahon, 2003). The three-year-old sample was biased toward females that were only tracked until their first breeding season and were not tracked over an entire annual cycle. One-year-old seals, from 12- to 24-months old, are referred to as ‘yearlings’, and after that as two- and three-year-olds.

### *Derivation of spatial and temporal data*

I used simple temperature-light loggers (LL; Platypus Engineering, Kingston, Tasmania, Australia) and temperature-time-depth recorders (TDRs; Wildlife Computers, Redmond, USA) to provide location data for the juvenile seals. The LL units were 60 x 45 x 25 mm and include an 8 megabit FLASH memory for storage of data. Light and temperature data were collected every 45 seconds. The temperature sensor had a resolution of  $\pm 0.2$  °C and a range of -12 to 31 °C. The TDRs were Mk3 - Mk7 models that measured temperature, depth (pressure) and light at the same sampling interval as the LLs.

Thirty-one juvenile seals were equipped with TDRs or LLs between 1999-2001 (3 in 1999/2000 and 28 in 2000/2001), encompassing 65 individual foraging trips. Over their annual cycle juvenile seals only have to return to land to moult (November ~ December) but they also return during the winter to haul-out, for reason which remain unclear (Hindell and Burton 1988; Kirkman et al. 2001; Wheatley 2001). Some seals may even return twice for this ‘winter’ or ‘mid-year’ haul-out. Seals were caught by hand as they were about to leave the island at the end of their annual moult using the technique of McMahon et al. (2000) and anaesthetised intravenously using prescribed doses of Telazol<sup>®</sup> (Chapter 2). The LLs and TDRs were attached to the hair on the dorsal surface of the seals using two-part epoxy (Araldite 268, Ciba Geigy).

### *Estimation of location from light levels*

At-sea locations were derived using geo-location software (Multi-trace, Jensen Software, Germany) that gave two locations per day (Bradshaw et al. 2002b). Positions that would have exceeded the maximum distance that could have been travelled per unit time ( $12.5 \text{ km h}^{-1}$  - McConnell et al. 1992; Bradshaw et al. 2002b) were excluded. During the equinox

periods (4 March - 14 April and 30 August - 14 October) when latitudes could not be estimated due to the invariance of day length, I used linear interpolation to the next reliable latitude to provide an estimate of the daily latitude. Daily positions were then filtered using a state-space Kalman location filter (Silbert et al. 2003).

#### *Spatial and temporal summary*

Once the location data were filtered, they were rasterized (i.e., converted from point data into gridded data) onto a 300 km x 300 km grid using Interactive Data Language (IDL 5.0 – Research Systems Inc., USA) routines. The size of the grid cells were set conservatively to allow for maximum distance that the seals could travel (between an average of 70–90 km d<sup>-1</sup>; McConnell and Fedak, 1996; Le Boeuf et al. 2000) and the errors associated with geo-location estimates (Bradshaw et al. 2002b; van den Hoff et al. 2002). For each grid cell, the time (h) spent within any grid cell for each individual was calculated. The data were further split into summer and winter to summarize temporal differences in time spent at sea among the oceanographic and fisheries management zones per age group. The seasons were defined by the annual cycle of the juvenile seals: ‘summer’ was from 1 December to 14 May, and ‘winter’ from 15 May to 30 November. The ‘summer’ period starts as the juveniles leave Macquarie Island at the end their annual moult for their first trip to sea (i.e., encompassing the austral summer). After this period, the rest of the year is defined as ‘winter’.

I calculated the time (h) spent by each individual within the relevant national Exclusive Economic Zones (EEZ) and CCAMLR-managed areas (Subareas 54.4.1, 88.1 and 88.2). I also did this for five oceanographic/ecological regions defined by major frontal systems within the study area (Orsi et al. 1995; Rintoul et al. 1997). These regions were: (1) Sub-tropical zone to the north of the Sub-tropical Front (STF), (2) Sub-Antarctic zone (SAZ) between the Sub-tropical Front and the Sub-Antarctic Front (3) the Polar Frontal zone (PFZ) between the Sub-Antarctic Front (SAF) and the Antarctic Polar front (PF), (4) Antarctic zone (AZ) between the APF and southern boundary of the Antarctic Circumpolar Current (SBDY) including the southern Antarctic circumpolar current front (sACCF), and (5) south of the SBDY as the high Antarctic zone (HAZ).

*Population estimates of regional use*

Using the daily locations I estimated the total number of seal-days in each of the management regions for the summer and winter periods by estimating numbers of individuals within each age group and the mean number of days at sea by those age groups. The numbers of individuals in each age group were estimated as 10,265 yearlings, 9,808 two-year-olds and 8,033 three-year-olds. These values were derived using a total population of 76,000 seals and assuming a stable age structure for the Macquarie Island population (McMahon et al. 2003).

**Results**

Over the entire study period, the yearlings spent on average  $289.8 \pm 11.0$  days at sea, the two-year olds spent  $300.2 \pm 8.0$  days at sea, and the three-year olds spent  $246.3 \pm 12.3$  days at sea. However, it should be noted that the three-year-olds' sample was biased toward females attempting to breed for the first time (9 females compared to 1 male) that had their tracking units removed before their post-breeding trip to sea. If included, this additional trip would have added  $\sim 77 \pm 1.5$  days (Hindell et al. 2003b) to their total time at sea. Yearlings travelled up to 2296 km from Macquarie Island while ranging from 126 °E to 165 °W and 41 to 66 °S. The two-year olds travelled up to 5076 km away, ranging from 115 °E to 122 °W and 44 to 72 °S. The three-year olds travelled up to 4084 km away from the island and ranged between 105 °E to 123 °W and from 43 to 72 °S. Overall, the juvenile seals spent less time at sea in the 'summer' period than in the 'winter' period ( $114 \pm 10$  and  $163 \pm 23$  days, respectively; Table 3.1).

*Table 3.1. The number of days (mean  $\pm$  SD) spent at sea by the different age juvenile southern elephant seals from Macquarie Island in summer and winter seasons.*

Age	n	Total		Summer		Winter	
		Mean	SD	Mean	SD	Mean	SD
1	15	289.8	11.0	110.3	7.1	179.5	7.7
2	6	300.2	8.0	127.2	10.4	173.0	11.4
3	10	246.3	12.3	112.9	7.3	133.5	8.4
Overall	31	277.8	24.8	114.4	10.0	163.4	22.7

*Oceanographic/Ecological Zones*

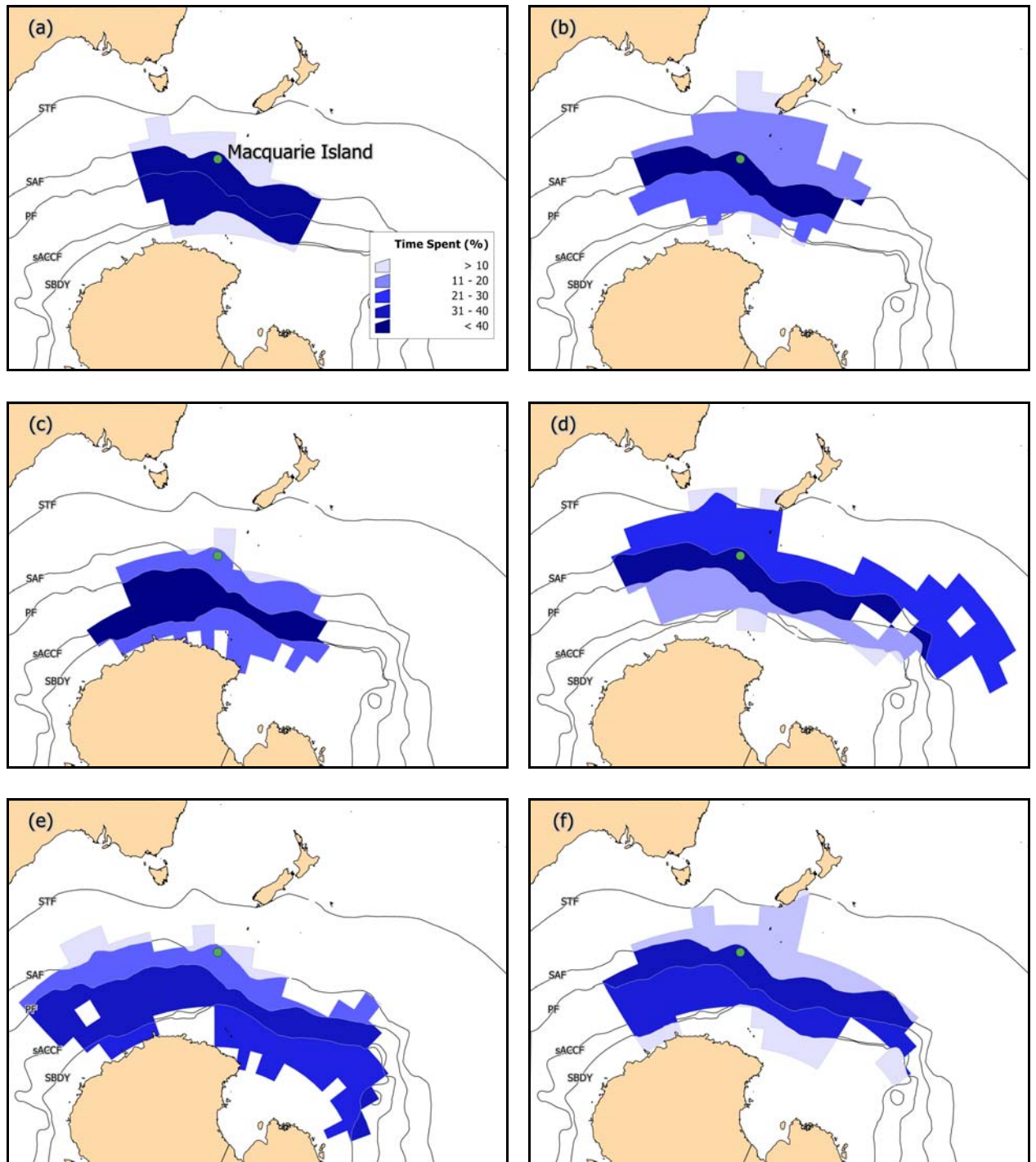
Overall, juvenile seals spent over 95 % of their time at sea during the summer period south of the Polar Front (Fig. 3.1), with the two- and three-year olds spending over  $\sim 25$  % of

their time in the high Antarctic zone (Table 3.2). In winter, juvenile seals spent less time in southern waters, but still spent ~75 % of their time south of the Polar Front; the one- and two-year olds spent ~25 % in the Sub-Antarctic zone. There was a clear pattern of older seals travelling farther south and farther away from Macquarie Island than younger seals in both summer and winter. However, in winter the two-year-old seals travelled farther from Macquarie Island mainly in the Sub-Antarctic and Polar Frontal zones, whereas the three-year olds did not travel as far but remained in more southerly waters.

#### *Managed Areas*

There were differences in the amount of time spent within the different management zones (Fig. 3.2) for each age group (Table 3.3). In summer, all age groups spent more than ~75 % of their time in managed regions. In winter one- and three-year old seals spent over ~65 % of their time in managed areas, but the two-year-old seals spent the majority (56 %) of their time in the unmanaged high seas. The one-year olds spent ~ 50 %, and the two- and three- year olds spent ~ 80 %, of their time in CCAMLR regions during the summer period. In winter, the amount of time in CCAMLR regions decreased, with the one- and two-year olds spending ~ 30 % of their time in the CCAMLR areas; whereas, the three-year olds remained farther south and spent ~ 60 % of their time in these regions.

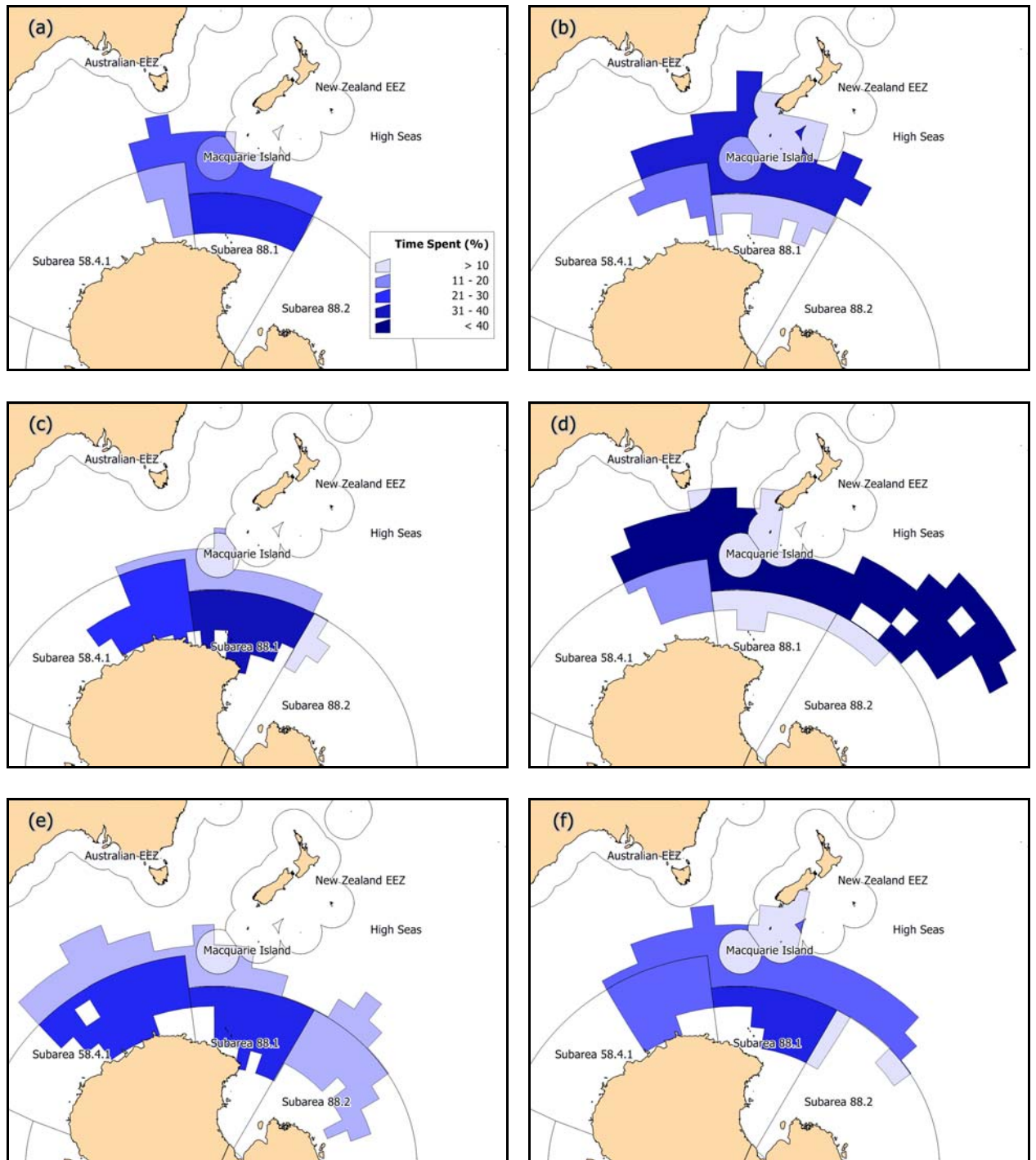
The number of seal-days at sea for all juvenile seals (28,108 seals) in the summer and winter periods were 3,286,610 and 4,611,041 days, respectively. In summer, juveniles are estimated to have spent 2,266,297 days in the CCAMLR managed areas, 628,262 days in the unmanaged high seas and 365,532 days in the Australian EEZ (Table 3.4). In winter, the pattern was different, and juveniles are estimated to have spent the most time in the high seas (1,901,839 days), CCAMLR Subareas (1,752,738 days) and the remainder of their time in the Australian and New Zealand EEZs (Table 3.4).



*Fig. 3.1a–f. Map showing the proportional time at sea spent in the oceanographic/ecological zones of the Southern Ocean for 1-, 2- and 3-year-old southern elephant seals from Macquarie Island in summer (a, b and c, respectively) and winter (d, e and f, respectively) with darker shading indicating more time spent in those regions. Also shown are the mean positions of the oceanographic boundaries of the Southern Ocean (STF, SAF, PF, sACCF and the SBDY) used to define the oceanographic/ecological zones.*

*Table 3.2. The percentage of time spent in the different ecological zones in the summer and winter for the 31 one-, two- and three-year-old southern elephant seals in this study. Also shown is the mean time (h)  $\pm$  SD within each zone.*

Age	Sub-Tropical Zone			Sub-Antarctic Zone			Polar Frontal Zone			Antarctic Zone			High Antarctic Zone		
	%	Mean	SD	%	Mean	SD	%	Mean	SD	%	Mean	SD	%	Mean	SD
Summer															
1	0.0	0.0	0.0	3.3	89.8	101.9	46.9	1242.6	380.9	46.3	1225.5	430.9	3.5	90.2	145.7
2	0.0	0.0	0.0	0.1	2.8	6.8	25.3	740.2	594.4	50.1	1547.7	541.9	24.6	761.7	630.2
3	0.0	0.0	0.0	1.0	26.1	62.6	24.0	658.4	619.6	39.9	1081.5	585.0	35.0	942.6	785.9
Winter															
1	0.3	14.2	55.0	20.5	885.8	1047.0	54.4	2339.1	827.7	24.6	1061.9	934.3	0.1	5.9	15.9
2	0.6	24.0	48.8	31.4	1318.0	948.0	45.9	1929.1	1163.0	18.2	726.6	974.6	3.9	154.2	327.2
3	0.3	10.5	33.3	12.8	429.0	640.6	41.1	1312.9	806.1	36.6	1161.3	770.9	9.2	289.6	299.1



*Fig. 3.2a-f. Map showing the proportional time at sea spent in the managed areas (CCAMLR subareas 54.4.3, 88.1 and 88.2 and the 200 nm exclusive economic zone for Australia, Macquarie Island and New Zealand) of the Southern Ocean for 1-, 2- and 3-year-old southern elephant seals from Macquarie Island in summer (a, b and c, respectively) and winter (d, e and f, respectively) with darker shading indicating more time spent in those areas.*

Table 3.3. The proportion of time spent in the different managed areas in the summer and winter for one-, two- and three-year-old southern elephant seals in this study. Also shown is the mean time ( $h$ )  $\pm$  SD within each zone.

Age	High Seas			CCAMLR			Australian EEZ			New Zealand EEZ			Overall Managed Areas		
	%	Mean	SD	%	Mean	SD	%	Mean	SD	%	Mean	SD	%	Mean	SD
Summer															
1	26.8	708.6	258.1	50.4	1334.1	663.6	20.7	548.5	330.0	2.1	56.8	82.1	73.2	1939.5	523.9
2	16.3	469.0	411.7	77.0	2383.8	915.2	6.7	199.6	144.6	0.0	0.0	0.0	83.7	2583.4	742.2
3	14.6	398.9	425.0	79.9	2155.6	1001.3	5.3	147.4	117.5	0.3	6.6	20.4	85.4	2309.6	781.7
Winter															
1	36.8	1601.1	897.3	34.4	1487.0	885.2	17.5	733.2	577.6	11.3	485.7	1001.3	63.2	2705.9	810.9
2	56.4	2340.6	1097.7	27.6	1147.4	627.0	7.5	311.0	182.5	8.5	352.9	685.3	43.6	1811.3	528.8
3	24.3	778.3	731.2	61.1	1935.6	1011.4	7.4	236.4	165.0	7.1	253.0	623.6	75.7	2425.0	795.0

*Table 3.4. The estimated total number of seal days spent in the managed fisheries areas by the Macquarie Island population of one-, two- and three-year-old southern elephant seals. Also shown are the population estimates for each age group calculated from a total population of 76000 seal assuming the stable age structure from McMahon (2003) and the mean number of days at sea for each age group.*

Age	Number of seals	High Seas	Australian EEZ	Macquarie Island EEZ	New Zealand EEZ	Subarea 58-4-1	Subarea 88-1	Subarea 88-2
Summer								
1	10265	0.0	303091.1	234617.3	24307.8	189638.9	380988.1	0.0
2	9808	0.0	191649.2	81587.2	0.0	373709.5	516821.0	83640.8
3	8033	0.0	133522.2	49327.2	2210.7	286855.9	296719.0	137923.8
Overall	28106	0.0	628262.5	365531.7	26518.5	850204.2	1194528.2	221564.6
Winter								
1	10265	0.0	684811.3	313587.2	207746.4	400420.3	235569.2	0.0
2	9808	1504.4	956528.5	125588.0	144229.1	319463.2	121820.0	27611.5
3	8033	0.0	260499.4	79133.1	84675.5	256990.0	363387.0	27476.5
Overall	28106	1504.4	1901839.1	518308.3	436651.0	976873.5	720776.2	55088.0

## Discussion

Our results show that the juvenile component of the southern elephant seal population at Macquarie Island, though hauling out on a subantarctic island, spent a large amount of time in managed fisheries areas (especially CCAMLR Subareas 54.4.1, 88.1 and 88.2).

Although CCAMLR has been successful in the conservative management of the krill-based ecosystem, much of the region has been subject to relatively low harvesting rates (Nicol and Endo 1999; Nicol and Foster 2003), although possible increases in fishing have been predicted (Goldsworthy et al. 2001; Nicol and Foster 2003). At present, the management framework has focussed mainly on the krill-based ecosystem south of the sACCF because krill showed the greatest potential for harvesting and they are an important source of food for vertebrate predators (Nicol and Endo 1999; Nicol et al. 2000). The pelagic region, on the other hand, has been more difficult to survey and its importance in terms of potential biomass may have been under-estimated. Indeed, only recently have data become available that reflect the complex community structure and potentially high biomass of secondary producers (Hosie et al. 2003) that support higher-order predators foraging in this region.

### *Seasonal habitat use*

I found a clear pattern in the seasonal use of the Southern Ocean by juvenile elephant seals. In the summer period, juvenile seals spent around 90 % of their time south of the Polar Front and 70 % within CCAMLR-managed areas. In winter however, juveniles spent the majority (around 75 %) of their time between the Polar Front and the southern boundary of the Antarctic Circumpolar Current and ~ 37 % of their time in CCAMLR-managed areas. Our results contrast with the summer use by adult females that spend the majority (46 %) of their time in the zone lying between the Sub-Antarctic and Polar fronts (Hindell et al. 2003b). Additionally, younger seals (8 and 18-months old) spent only 27 % of their time in CCAMLR-managed areas, and ~ 23 % in Australian and New Zealand EEZs (van den Hoff et al. 2002).

Some caution should be exercised when comparing the different spatial use patterns for different age classes. Hindell et al. (2003b) determined that the minimum sample size required to establish 95 % coverage of the total area of the ocean used by adult females was 25 individuals. Even though the sample size in our present study represents the largest to date for juvenile seals, our samples sizes were still relatively small, particularly when

divided into age and season classes. Thus, our estimates of total area used by the juvenile seals may be underestimated. Despite subtle differences in the timing of at-sea movements for the different age classes, our results nonetheless confirm that juveniles in general appear to use different areas of the Southern Ocean compared to adult females (although there is some overlap).

### *Oceanographic and ecological habitat use*

During both seasons the juveniles spent much of their time in the Polar Frontal and Antarctic zones, which suggest that these regions are important foraging areas. Previously, this region has been considered relatively oligotrophic; however, recent studies have highlighted the high abundance and species richness of zooplankton within these zones (Hosie et al. 2003). Although our understanding of elephant seal diet is still rudimentary (Green and Burton 1993; Slip 1995; Daneri et al. 2000; Santos et al. 2001; Daneri and Carlini 2002; Bradshaw et al. 2003), primary prey species of elephant seals such as squid and fish are thought to depend heavily on zooplankton within this region (Dauby et al. 2003).

### *Current and potential fisheries overlap*

At present there are three commercial fisheries that target known prey of southern elephant seals from Macquarie Island: 1) Patagonian toothfish (*Dissostichus eleginoides*) have been reported in the diet of elephant seals (Slip, 1995; Burton and van den Hoff, 2002; Chapter 5) and in fisheries around Macquarie Island, in the New Zealand EEZ, and in CCAMLR Statistical Subareas 88.1 and 88.2; 2) The New Zealand squid fishery over the Campbell Plateau; 3) The krill fishery for *E. superba* in CCAMLR Statistical Subareas 54.4.1, though krill are a minor component in the diet of southern elephant seals (van den Hoff et al. 2003; Bradshaw et al. 2003). However, if there is expansion of existing fisheries or new resources are found then it is likely that there will be some dietary overlap with this generalist predator that can respond to changes in prey availability (Piatkowski et al. 2002).

Southern elephant seals are major consumers of squid and fish in the Southern Ocean (Clarke 1983; Boyd et al. 1994; Bradshaw et al. 2003; Hindell et al. 2003b), and recent modelling has suggested that elephant seals consume between 19 - 36 % of the entire squid

biomass taken by all whales, seals and birds combined in the Southern Ocean (Clarke, 1983; Santos et al. 2001). The use of conventional techniques (Green and Burton, 1993; Slip, 1995; van den Hoff et al. 2003) and fatty acid signature analysis (Brown et al. 1999; Bradshaw et al. 2003) have identified that the seals are generalist feeders. A recent study of the diet of adult females has also been able to attribute general feeding patterns relative to different foraging areas (Bradshaw et al. 2003).

Better information on spatial and temporal variation in seal diet combined with detailed, age-specific information on foraging extent and behaviour are needed to improve current models of prey consumption by this apex marine predator. Juvenile southern elephant seals are an important component of the population influencing change in population numbers (McMahon et al. 2004) associated with resource limitations, which has also been proposed by Trites and Donnelly (2003) for the declining Steller sea lion population of the north Pacific. This, coupled with their wide-ranging at-sea distribution, makes elephant seals a potentially important indicator of both natural and anthropogenic baseline variability within the Southern Ocean marine ecosystem. Thus, elephant seals represent a useful monitoring species for the open ocean pelagic system of the Southern Ocean that will lead to better understanding and management of this poorly described bio-physical environment.

## Summary

The foraging distribution of marine predator populations is important for effective modelling and management of pelagic marine systems. I tracked 31 juvenile southern elephant seals from Macquarie Island (158° 57'E, 54° 30'S) over their annual post-moult and mid-year trips to sea. I calculated the amount of time spent in regional fisheries management areas and within bounded oceanographic regions. During the austral summer, juvenile seals spent over 90 % of their time south of the Antarctic Polar Front and ~ 80 % within fisheries management regions (CCAMLR and Exclusive Economic Zones). In winter, seals spent ~ 75 % of their time in the region bounded by the Antarctic Polar Front and the southern boundary of the Antarctic Circumpolar Current, and ~ 60 % within fisheries-management regions. The time spent per region differed significantly between summer and winter. Our results demonstrate that juvenile southern elephant seals from

Macquarie Island spent more time south of the Antarctic Polar Front and within fisheries management areas than previously suspected.

Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals (*Mirounga leonina*).

## Introduction

For nearly half a century niche theory has provided a framework for explaining competition within ecological communities and the mechanisms by which they function (Pianka 1981; Bolnick et al. 2003). A major force in driving community structure is derived from inter-specific competition for resources (Schoener 1986); more recently intra-specific competition has been identified as a significant component in the evolution of niche width (Polis 1984). For many species, groups of individuals classed according to age, sex and morphology exhibit significant variation in foraging behaviour and diet specialization (Bolnick et al. 2003), or even through individual's variation and all contribute to the definition of the species' or population's niche width. An important component in the evolution of population dynamics is phenotypic variation within a population that occurs between age and sex classes (Schoener 1986). Ontogenetic niche shifts (Woodward and Hildrew 2002) have been proposed for many species as the major component of total niche width attributed to age/size structure (Warren 1996; Williams and Martinez 2000; Bolnick et al. 2003).

Resource partitioning may function through interference competition, or exclusion from resources or habitat as an evolutionary trait of sexual selection (Polis 1984). Although this usually increases a surviving individual's fitness, the resulting increase in competition may restrict juvenile recruitment during times of resource limitation. Therefore, ontogenetic shifts in morphology, habitat use and foraging behaviour may promote population stability more effectively over evolutionary time (Polis 1984). The reduction of intra-specific competition through resource partitioning has been observed for many species over a range of spatial scales, especially when resources are limited and environmental predictability is low (Perry 1996; Kato et al. 2000; Wikelski and Wrege 2000; Bowen et al. 2002; Pearson et al. 2002; Bradshaw et al. 2003). For example, size-specific resource partitioning in little brown bats (*Myotis lucifugus*) correlates to shifts in habitat use and diet with ontogenetic development (Adams 1996).

The distribution of biological resources within the Southern Ocean is highly variable, unpredictable and patchy (Constable et al. 2003). This variability and pronounced patchy distribution may require marine species to develop intra-specific niche specialization to maximize the probability of securing resources for growth and reproduction. Although

some studies have documented ontogenetic and morphometric shifts in the diving behaviour of marine vertebrates, most have focused on developmental physiology and behavioural aspects (Burns 1999; Baechler et al. 2002) rather than the ecological or evolutionary function of these shifts. One recent study has shown that on a local scale, marine iguanas (*Amblyrhynchus cristatus*) have developed ontogenetic foraging niches that increase probability of survival in an unpredictable environment (Wikelski and Wrege 2000).

Southern elephant seals (*Mirounga leonina*) are wide-ranging, deep-diving predators within the Southern Ocean ecosystem that spend more than 80% of their annual cycle at-sea and are large consumers of fish and squid (Bradshaw et al. 2003; Hindell et al. 2003). The population of *M. leonina* at Macquarie Island has been declining for reasons that are still unclear (Hindell et al. 1994), though is most likely due to changes in food availability and distribution (McMahon et al. 2004). Recently, it has been shown that juvenile (1 to 4 years) survival is the most important factor affecting the population rate of change (McMahon et al. 2003). Thus, it appears that the potential for ontogenetic shifts in foraging behaviour and diet through changes in morphology and physiology might have important implications for the ecological dynamics of this population in particular (Chapter 3; McMahon et al. 2004). Until recently, knowledge of juvenile southern elephant seals was restricted to studies of individuals ashore (Le Boeuf and Laws 1994; Wheatley 2001). The annual cycle of juveniles is unusual in that in addition to the annual moult (November to January) it incorporates a facultative mid-year time ashore (April to August). The purpose of this haul-out is unclear; however, the possibilities include physiological restrictions, parasite reduction and social stimulation (Ling and Bryden 1981; Neumann 1999). Another function could be that the mid-year haul-out may have evolved as a by-product of intra-specific resource partitioning through ontogenetic shifts in foraging ability. The foraging ecology of southern and northern elephant seals has been studied extensively (Slip 1997; Slip et al. 1994; Le Boeuf 1994b; Stewart 1997) but only two studies have described the at-sea movements of non-naïve (> 1 year-old) southern juveniles (van den Hoff et al. 2002; Chapter 3). For both species there are profound physiological and behaviour changes between juveniles and adults (Le Boeuf et al. 2000).

In this paper I examine the foraging patterns of juvenile southern elephant seals and test the hypotheses that as juveniles mature (1) the different age groups will use different regions of the Southern Ocean through differences in the haul-out patterns, durations of time spent at sea, distances travelled, and the total area used by individuals grouped according to age and sex, and (2) individuals demonstrate fidelity to foraging areas that reinforce spatial separation. Observed patterns of foraging are discussed in light of the possible evolutionary mechanisms responsible for ontogenetic resource partitioning that may have occurred in a species demonstrating some of the greatest horizontal and vertical movements of any mammal.

## Materials and methods

The southern elephant seal population at Macquarie Island (158° 57'E, 54° 30'S) has been the focus of a long-term mark-recapture demographic study since 1993 (McMahon et al. 2003). I studied juvenile seals, of known age, between one and four years old and having no breeding experience. Seals from one to two years are referred to as 'yearlings' and after that, as two- or three-year-olds.

I used temperature-light loggers (LL; R. Hansworth, Kingston, TAS, Australia) and temperature-depth-recorders (TDRs; Wildlife Computers, Redmond, USA) to provide location data for the juvenile seals. The LL units were 60 x 45 x 25 mm in size and had an 8-megabit FLASH memory for storage of data. Light and temperature data were collected every 45 seconds. The temperature readings had a resolution of  $\pm 0.2$  °C and a range of -12 to 31 °C. The TDRs used included Mk3, Mk5, Mk6 and Mk7 models and measured temperature and light at the same sampling interval as the LLs. All units weighed less than 350 g, which represented  $< 0.5$  % of the departure mass of the smallest seal in the study (78 kg).

Forty-eight juvenile seals were equipped with TDRs or LLs between 1999-2001 (16 in 1999/2000 and 32 in 2000/2001) encompassing 83 individual foraging trips. Seals were caught as they were about to leave the island at the end their annual moult. During captures all restraint and disturbance to seals were kept to a minimum. Seals were caught and anesthetized intravenously and using prescribed doses (Chapter 2) of tiletamine and zolazepam (Telazol<sup>®</sup>, Forte Dodge, Castle Hill, NSW, Australia).

Once anaesthetized, the LLs and TDRs were attached by gluing them to the hair on the dorsal surface of the seals between the shoulder blades using epoxy (Araldite 268, Ciba Geigy). Over the study period, the beaches on and near the northern isthmus of the island were searched daily for marked individuals returning ashore to calculate the haul-out patterns of these age groups and for individuals with data-logging units. The units were retrieved either by capturing the seals when the seals returned to shore, or by collecting the units from the beach after they were shed during the molt. LL and TDR data also contributed to the separation of the land and sea phases for the calculation of haul-out patterns.

#### *Estimation of location from light levels*

At-sea locations were derived using geo-location software (Multi-trace, Jensen Software, Germany) giving two locations per day. These data were filtered to exclude positions that would have exceeded the maximum distance that could have been travelled ( $12.5 \text{ km h}^{-1}$ , Bradshaw et al. 2002b). During the equinox periods (4 March - 14 April and 30 August - 14 October) estimates of longitude are unaffected but latitudes could not be estimated due to the invariance of day length. During this period, the juvenile seals are generally in transit to and from Macquarie Island to their foraging areas, during which their travel in a direct path. I used linear interpolation of latitude to the next most reliable location to provide an estimate of the daily location (van den Hoff et al. 2002; Bradshaw et al. 2002). Daily positions were filtered using a state-space Kalman location filter (Sibert et al. 2003). This time-dependent model of the variance in geo-location estimates (Sibert et al. 2003) was used to provide realistic estimates of *in situ* movement parameters from geo-location positions while the seals were at sea. Light-derived geo-location data have inherent spatial errors up to  $\pm 350 \text{ km}$  (van den Hoff 2002; Bradshaw et al. 2002b) and other parameters derived from them retain these errors.

#### *Use of location data and mean migration parameters*

To compare location data among sex/age groups, I calculated the following maximum mean migration parameters per individual: duration of a trip to sea, maximum distance from Macquarie Island, total trip distance and daily rates of travel. I also calculated the bearing to the position of maximum distance to indicate the major directional component

of each foraging trip (Bradshaw et al. 2004) which simply represents the path of the migration.

I compared these parameters between the different age/sex groups using one-way general linear models (GLM) for only seals ( $n = 42$ ) with complete trips to sea ( $n = 76$ ). Some seals recorded data for consecutive trips to sea within the study period so I compared an individual's maximum distance reached and duration of different trips using repeated-measures ANOVA, (2 trips:  $n = 10$ ; 3 trips:  $n = 12$ ) to determine if all trips to sea could be included in the analyses. These were found to be the same for sequential trips and so I pooled the data to improve statistical power. I also tested the hypothesis that individuals showed fidelity to foraging areas using the bearing to the location of maximum distance in trip  $i+1$  versus to that of trip  $i$  for an individual's sequential trips to sea using a linear regression model (Bradshaw et al. 2004).

#### *Spatial summary*

Once the location data were filtered, they were rasterized onto a 300 km x 300 km grid (IDL 5.0 – Research Systems Inc., USA). The size of the grid cells were set to allow for maximum distance that the seals could travel (between an average of 70–90 km d<sup>-1</sup>; Le Boeuf et al. 2000) and the errors associated with geo-location (Bradshaw et al. 2002b; van den Hoff et al. 2002). For each grid cell, a central longitude and latitude were produced and the time (h) spent within any grid cell for each individual. The data for all seals ( $n = 48$ ) were split into 14-day blocks for temporal differences in spatial overlap and the mean maximum distance between age/sex groups to be examined using a series of Kruskal-Wallis tests (Bonferroni corrected;  $p < 0.002$ ).

#### *Total area used - age and sex comparisons*

I used one-way GLM to test for differences between age/sex groups in the total number of days spent at sea and the total area used. For these analyses, only seals ( $n = 31$ ) with complete data for the period between the end of the annual moult and the following moulting season or first breeding season (December to November). There were too few data from each year to examine annual effects statistically, so data from both years were pooled. The areas used by individuals were calculated and analysed in the same manner as the other migration parameters.

### *Time spent within oceanographic regions*

I calculated the time spent by each individual within five distinct oceanographic regions defined by frontal systems within the study area (Orsi et al. 1995; Rintoul et al. 1997) as a proportion of their total time at sea, and compared them using a one-way GLM. The regions were defined as the; 1) Sub-tropical zone to the north of the Sub-tropical Front (STF), 2) Sub-Antarctic zone (SAZ) between the Sub-tropical Front and the Sub-Antarctic Front 3) the polar frontal zone (PFZ) between the Sub-Antarctic Front (SAF) and the Antarctic Polar front (APF), 4) Antarctic zone (AZ) between the APF and southern boundary of the Antarctic Circumpolar Current (SBDY), and 5) south of the SBDY as the high Antarctic zone (HAZ).

## Results

### *Annual cycle patterns*

For the first mid-year haul-out, the yearlings arrived first (average arrival day = 4 April), followed by the two-year olds (1 May) and three-year olds (27 May). Some seals had a second mid-year haul-out, during which the yearlings of both sexes returned but only a two-year old male returned from the older age groups. Here, the mean arrival date for yearlings was 23 July, and 4 August for the two-year old male and mean residence time was almost half that of the first haul-out (Table 4.1). For the moult, the first to return were the two-year-olds (26 Nov), followed by the yearlings (1 Dec) and the three-year olds (3 Dec), but the differences were not significant as has been found in other studies with larger sample sizes (Hindell 1998; Wheatley 2001). The number of trips to sea varied with age: yearlings made ( $\bar{X} \pm \text{SD}$ )  $2.7 \pm 0.46$  trips, two-year olds made  $2.2 \pm 0.41$  trips, and three-year olds made  $1.1 \pm 0.32$  trips.

### *At-sea distribution*

The total area used by all seals over all trips to sea was 16,292,500 km<sup>2</sup> ( $n=83$  trips to sea) between 107° and 234 °E, and 34° and 71 °S (Fig. 4.1). The seals travelled predominantly to the southeast and southwest (Fig. 4.2), with a few travelling northwest. There was a significant difference (one-way ANOVA:  $F_{2,25} = 4.03$ ;  $P < 0.03$ ,  $n = 31$ ) between the mean total area used by the different age groups; a *post-hoc* LSD test indicated that yearlings used a significantly smaller area ( $2,392,833 \pm 533,697$  km<sup>2</sup>) than two- and three-year olds, but there was no difference between the two older ages (combined mean area = 3,537,188

$\pm 1,319,271 \text{ km}^2$ ; Fig. 4.1). There were no significant sex or interaction effects (one-way ANOVA:  $F_{1,25} = 0.99$ ;  $P < 0.76$  and  $F_{2,25} = 0.11$ ;  $P < 0.89$ , respectively).

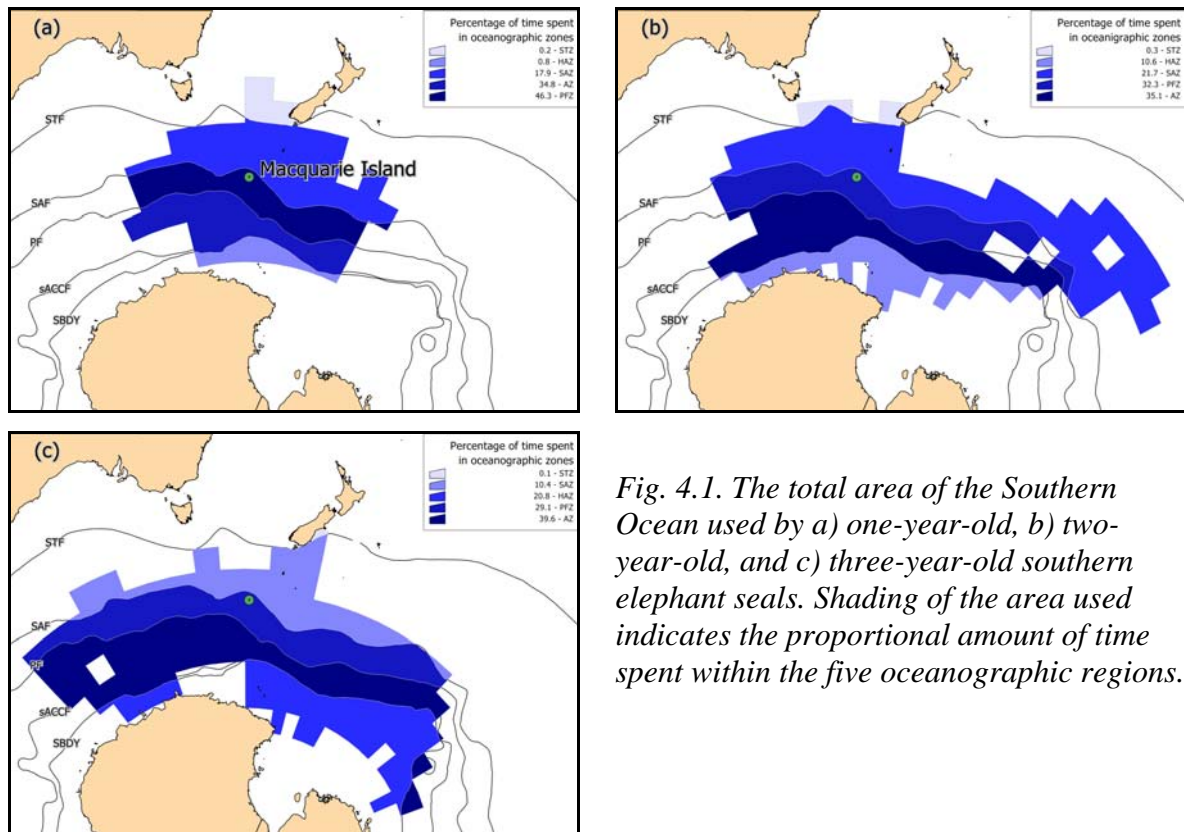


Fig. 4.1. The total area of the Southern Ocean used by a) one-year-old, b) two-year-old, and c) three-year-old southern elephant seals. Shading of the area used indicates the proportional amount of time spent within the five oceanographic regions.

Table 4.1. The arrival date and residence times of the juvenile seals from tracking unit data, shown as  $\bar{X} \pm SD$  (days), for 15 yearlings, 16 two-year olds and 16 three-year-old seals.

Haul-out	Age	n	Mean arrival date	Residence time (days)
1 MY	1	15	3 April $\pm 11.97$	25.13 $\pm 3.98$
	2	7	1 May $\pm 26.45$	29.29 $\pm 4.5$
	3	1	26 May	46
2 MY	1	11	24 July $\pm 17.03$	11.64 $\pm 3.33$
	2	1	4 August	12
	3	-	-	-
Moult	1	15	1 December $\pm 8.85$	30.47 $\pm 5.63$
	2	16	26 November $\pm 10.09$	36.25 $\pm 5.86$
	3	16	3 December $\pm 9.87$	47.69 $\pm 5.34$

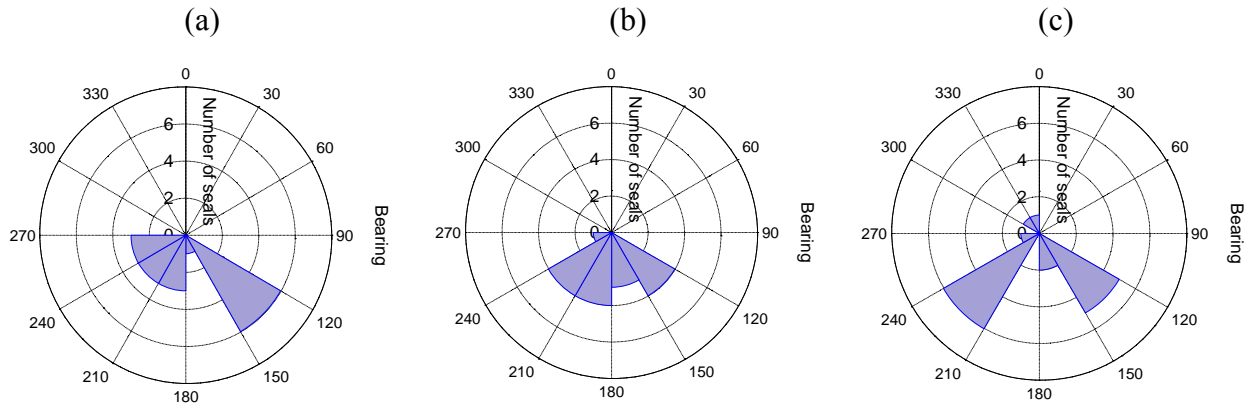


Fig.4.2. The bearing of travel for a) one-year-old, b) two-year-old, and c) three-year-old southern elephant seals.

#### *Time spent within oceanographic regions*

Yearlings spent around 99% of their time in the SAZ, PFZ and AZ, and less than 1% of their time south of the SBDY in the HAZ. Two-year olds spent approximately 89% of their time in the SAZ, PFZ and AZ, and 11% in the HAZ. Finally, the three-year olds spent 80% in the SAZ, PFZ and AZ, and 20% in the HAZ.

#### *Individual behaviour*

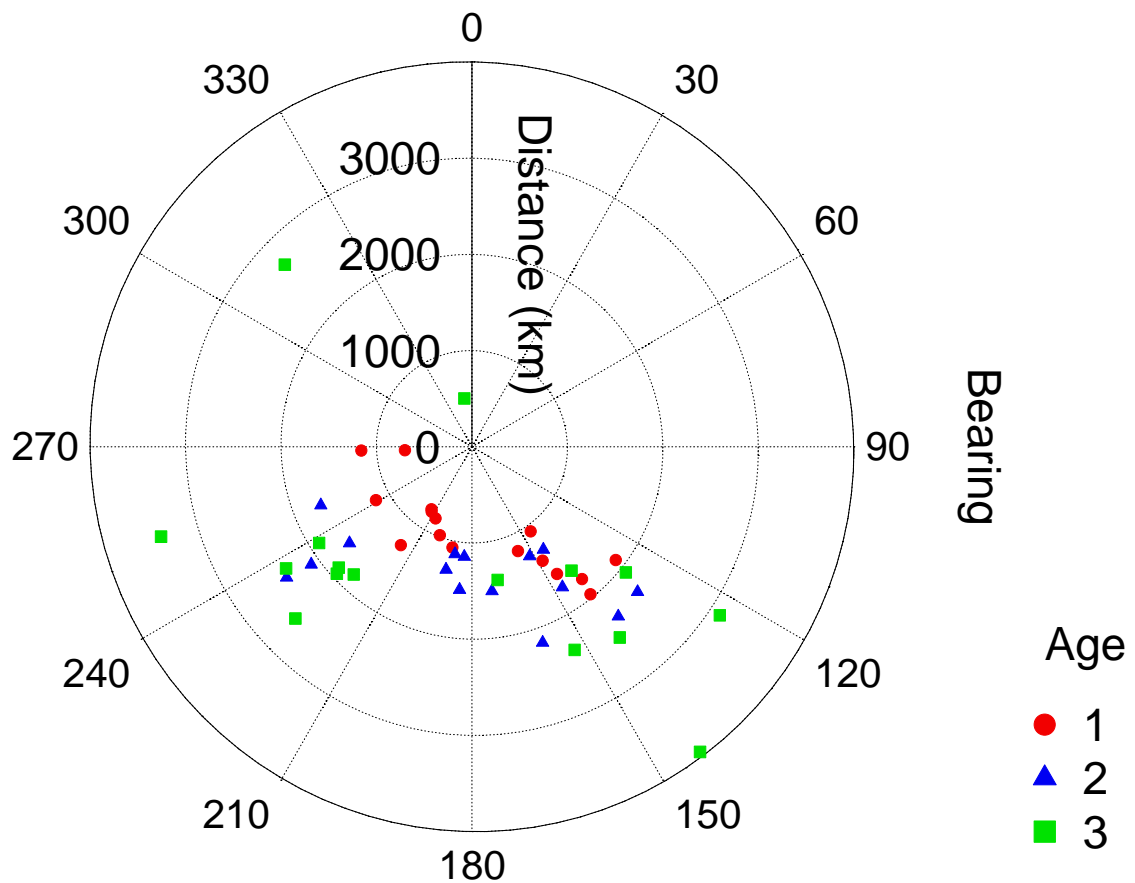
There were significant differences between migration parameters for the different age/sex groups (Table 4.2). Older seals travelled farther from Macquarie Island, than younger seals (one-way ANOVA:  $F_{2,40} = 3.344$ ;  $P = 0.001$ ,  $n = 42$ ; Fig. 4.3). This difference was due largely to the younger seals making shorter trips (duration) than older seals (one-way ANOVA:  $F_{2,40} = 19.581$ ;  $P < 0.001$ ), also younger males and female made similar trips but older females made longer trips than males (one-way ANOVA:  $F_{1,41} = 3.276$ ;  $P = 0.002$ ). Younger seals did not travel as far, (total distance travelled) and used a smaller area than older seals (one-way ANOVA:  $F_{2,40} = 3.073$ ;  $P = 0.003$  and  $F_{2,40} = 3.212$ ;  $P = 0.002$ , respectively), and again younger males and female made similar trips but older females made longer trips than males (one-way ANOVA:  $F_{1,41} = 2.349$ ;  $P = 0.024$ ). However, the daily rate of travel (total distance travelled/trip duration) was similar for all age/sex groups.

Seals tracked over sequential migrations had the same direction of travel for each trip regardless of whether the seals made two (linear regression: bearing of trip one to two:  $F_{1,9} = 23.213$ ,  $P = 0.001$ ,  $R^2 = 0.74$ ,  $n = 10$ ) or three trips to sea (linear regression: bearing of

trip one to two:  $F_{1,11} = 26.804$ ,  $P < 0.001$ ,  $R^2 = 0.73$ ; trip two to three:  $F_{1,11} = 10.281$ ,  $P = 0.009$ ,  $R^2 = 0.51$ ,  $N = 12$ ).

*Table 4.2. The migration parameters measured for the different age juvenile seals, shown as  $\bar{X} \pm SD$ .*

Age	Sex	n	Maximum distance (km)	Duration of trip (days)	Total distance traveled (km)	Area covered (km <sup>2</sup> )
1	F	11	1432 $\pm$ 278	196 $\pm$ 125	11985 $\pm$ 4488	1781818 $\pm$ 509116
	M	5	1586 $\pm$ 559	119 $\pm$ 102	12334 $\pm$ 4672	1592500 $\pm$ 433103
2	F	5	1999 $\pm$ 685	195 $\pm$ 145	16746 $\pm$ 7664	2082500 $\pm$ 755141
	M	5	2283 $\pm$ 1498	164 $\pm$ 123	12697 $\pm$ 4598	2474500 $\pm$ 1389714
3	F	11	2518 $\pm$ 717	249 $\pm$ 228	21388 $\pm$ 5683	3017955 $\pm$ 1158610
	M	5	1691 $\pm$ 812	141 $\pm$ 115	12646 $\pm$ 3422	1911000 $\pm$ 712188



*Fig. 4.3. The maximum distance reached in the first trip to sea by the different age juvenile southern elephant seals, where circles represent one-year olds, triangles two-year olds and squares three-year-old seals.*

*Temporal variation in regional use*

There was a clear pattern of temporal and spatial segregation with age using maximum distance travelled from the island per 14-day time block (Fig. 4.4). Yearlings and two-year olds left Macquarie Island in December and moved approximately  $1146 \pm 403$  km and  $1457 \pm 478$  km away, respectively. Three-year olds left in January, potentially travelling through the areas used by the younger seals as they left the Island; however, once they reached the middle phase of their trip the overlap was minimal. The one-year-old seals remained relatively closer to MI at all times and returned earlier for their initial or only mid-year haul-out. The two-year olds returned for their haul-out later, but travelled farther from MI in their following trip to sea. Due to the low sample size of this age group after their mid-year haul-out, the maximum distance was not significantly different from those of the other age-groups; however, the pattern is consistent with that of the one and three year-olds. The three-year-old seals travelled farthest from MI and returned slowly to MI (but only one male was tracked after the mid-year haul-out). Thus, the maximum distance pattern was dominated by females having one trip to sea that returned in September/October to pup. In the mid-year the mean distance from MI remained large due to the variation in haul-out timings of the individuals of each age group.

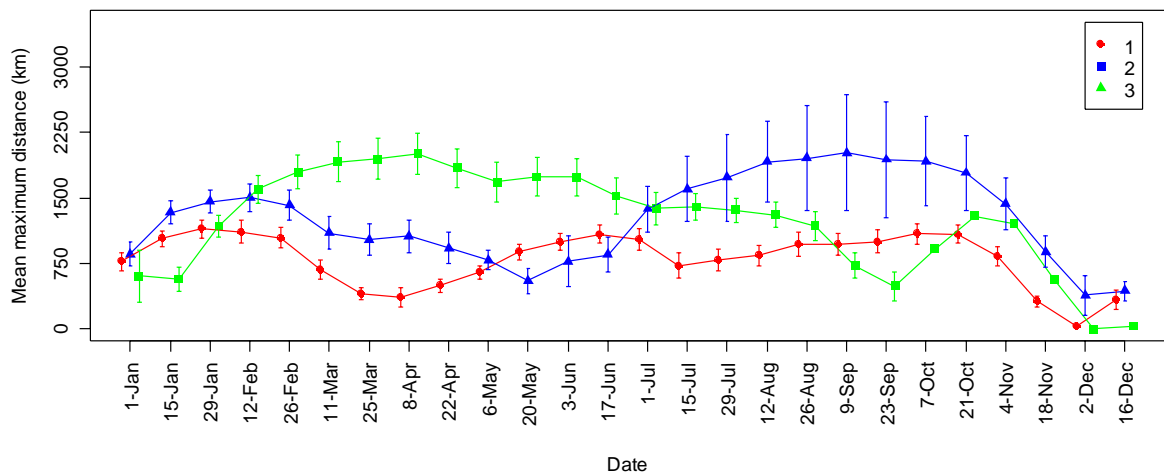


Fig. 4.4. The maximum distance ( $\bar{X} \pm SE$ ) reached each fortnight by the different age juvenile southern elephant seals, where circles represent one-year olds, triangles two-year olds and squares three-year-old seals.

## Discussion

Niche theory predicts, in an environment with limited or patchy resources, that selective pressures promote the evolution of generalist feeding behaviours and the reduction of intra-specific competition (Schoener 1986). Southern elephant seals have large energy requirements (Boyd et al. 1994), so their annual consumption of fish and squid is one of the highest for mammals and birds in the region (Hindell et al. 2003; Bradshaw et al. 2003). Thus, I hypothesize that the ability to find and sequester this considerable biomass from a patchy and unpredictable environment has resulted in the evolution of ontogenetic niche shifts. This process may have reduced local competition that then increased an individual's probability of foraging success as found for harbour seals (Iverson et al. 1997; Frost et al. 1998). I found a clear segregation in the use of the Southern Ocean by juvenile southern elephant seals over the course of their annual foraging trips. As the seals aged they made fewer, but longer trips to sea, travelled farther and spent more time closer to Antarctica. Further to this, the haul-out patterns and at sea distribution of adults, not studied here, has shown that during late summer adult seals are ashore to haul-out (Hindell and Burton 1991) and then while at sea are mostly foraging in high Antarctic waters (Hindell et al. 1991; Slip et al. 1994; Bradshaw et al. 2004). For many dimorphic species of marine mammals there are clear sex differences in foraging migrations or strategies (Boyd 2000; Le Boeuf et al. 2000; Beck et al. 2003b). The lack of strong sex differences in foraging behaviour is probably indicative of the lack of dimorphism during the juvenile years but may be due to our small sample sizes. However, it is unlikely that ecological sexual dimorphism is an important factor until closer to breeding age when male and female body sizes diverge dramatically. Exclusion and interference competition are unlikely due to the large range over which this species travels, their presumed solitary feeding behaviour, and abundance of suitable haul-out space on the beaches of Macquarie Island (McMahon et al. 2004). However, male and female elephant seals from Heard Island and Iles Kerguelen haul-out at different sites which Burton (1985) suggested reflects foraging-area separation.

The observed haul-out pattern was similar to that described previously for this species (Hindell and Burton, 1988; Wheatley 2001), as were the distances travelled (Bradshaw et al. 2004; Field et al. 2001; McConnell et al. 2002; Slip et al. 1994; van den Hoff et al. 2002). However, in contrast to juveniles of the congeneric *M. angustirostris*, *M. leonina*

juveniles develop foraging patterns similar to their adults later in life. This may be due to the lower age of sexual maturity for *M. angustirostris* (Le Boeuf et al. 1996). For *M. angustirostris* it has been suggested that the direction of migration is set within the first year of life (Stewart 1997); however, for *M. leonina* the direction of travel is predominantly south-east in the first year followed by a change to south-west and south-east (van den Hoff et al. 2002; McConnell et al. 2002). As adults, female southern elephant seals show remarkable fidelity to foraging regions between years (Bradshaw et al. 2004). Our data suggest that migration directions are fixed as yearlings, as individuals gain experience, but distances travelled are limited by their size, physiology and haul-out pattern. Stewart (1997) also suggested that the divergence in migration between sexes occurs at puberty because of sexual dimorphism and selection pressures through increased energy requirements of males. However, I propose this divergence in migration among age and sex groups is more likely due to intra-specific resource partitioning because the behaviour is expressed well before the onset of puberty and sexual dimorphism.

Other studies have demonstrated that temporal segregation of activity budgets in marine species do exist. Atlantic humpback whales (*Megaptera novaeangliae*) segregate their use of the ocean by timing of their migrations from their geographically distinct foraging areas to the common breeding areas (Stevick *et al.* 2003), which are proposed to have evolved to influence the mating opportunities at the breeding areas. Other species such as seabirds (Furness & Birkhead, 1984), marine iguanas (*Amblyrhynchus cristatus* - Buttemer & Dawson 1993), bowhead whales (*Balaena mysticetus* - Cosens & Blouw 2003) and harp seals (*Phoca groenlandica* - Sergeant 1991) also demonstrate geographical and temporal displacement in their migrations.

I found a clear pattern in both the haul-out and at-sea behaviour with increasing age. Although it is unclear what mechanisms drive intra-specific resource partitioning, I hypothesize that the mid-year haul-out functions as a temporal regulator of time at sea, and therefore, the foraging ranges of individuals. An important factor in this pattern must be the energetic cost of returning to haul-out. It is unknown whether returning to haul out during the mid-year incurs any additional costs; but if it does, then the costs must be outweighed by the benefits of reduced intra-specific competition. There is support for this view because older, larger individuals can dive deeper and return less often to haul-out

than younger seals. Therefore, as seals grow they exploit a greater area of the foraging environment unavailable to younger, smaller age classes. Our data show a delay in the haul-out pattern with age as the seals grow and are able to remain at sea for longer. The ultimate limitation on ontogenetic niche shifts for juvenile seals appears to be rate at which they can grow. Furthermore, older juvenile males (five- and six-year olds) have a mid-year haul-out (Wheatley 2001), and yet have similar physiology and foraging patterns to adults, so returning to land reduces competition during foraging. Although the mid-year haul-out may serve no particular function directly, it may promote the reduction of intra-specific competition and promote and re-enforce the survival probability of seals participating.

Alternatively, juveniles constrained physiologically and morphologically return to the island to reduce energy consumption or for physiological development. Juvenile harbour seals have been shown to have a restricted capacity to deal with heat-loss (Thompson et al. 1998) so the mid-year return may provide a better thermal environment for smaller individuals. Body size has also been shown to influence foraging strategies of adults for many species of marine mammals (reviewed in Bowen et al. 2002) and determine the nature of their foraging migrations. Furthermore, in juveniles of other species, changes in morphology and physiology with size/ age may lead to reduced intra-specific competition between juveniles (Adams 1996; Wikelski and Wrege 2000; Spina 2000).

Though little is known about the distribution of this prey, elephant seals are opportunistic generalist feeders with a broad foraging niche (Whitehead et al. 2003). Additionally, the broad spatial scale over which this segregation was observed suggests that reduced foraging niche overlap may be supported by the availability of different prey aggregations relative to oceanographic regions (Field et al. 2001; Bradshaw et al. 2003; Hindell et al. 2003). I suggest that as foraging range increases so does the potential width of the overall foraging niche. Foraging in a patchy and unpredictable environment has resulted in the evolution of behaviours that maximize their probability of foraging successfully and reduces intra-specific competition. If there is an equal probability of locating prey successfully in a patchy environment, then it is likely that the seals would leave their terrestrial haul-outs and disperse toward regions of generally higher productivity. However, this strategy would also be influenced by ontogenetic factors such as morphological and physiological constraints or experience. I suggest that, rather than

travelling to specific feeding areas, Macquarie Island elephant seals travel in a general direction and forage opportunistically across the different oceanographic regions until prey patch is found and exploited. Their behaviour is then modified further by ontogenetic shifts, through growth and changes in physiology.

Though this is the first comparison of spatial distribution data for juvenile southern elephant seals and represents a snapshot of their behaviour in relation to inter-annual variation, I suggest that the different age/size classes have become individual ‘ecological species’ thorough ontogenetic shifts in foraging niche. This has resulted from both temporal and spatial separation of resource use where individuals avoid intra-specific competition. The most-likely mechanism for the development of these behaviours is the modification of the haul-out timing in an environment where there is additional energetic cost in returning to haul-out, in conjunction with normal developmental restrictions. Thus, this process has allowed these wide-ranging and opportunistically feeding seals to exploit different oceanographic regions and increase their foraging niche width. Even with small sample sizes, sex differences also became evident with age due to the nature of sexual dimorphism shown within this species increasing the ecological separation. Future study of southern elephant seal diet, growth, physiology and diving behaviour may contribute to a better understanding of the function of the mid-year haul-out and how competition structures the marine community of the Southern Ocean.

## Summary

In highly dynamic and unpredictable environments such as the Southern Ocean, species that have evolved behaviours that reduce the effects of intra-specific competition may have a selective advantage. This is particularly true when juveniles face disadvantages when foraging due to morphological or physiological limitation, such as in the case of many marine mammals. I tracked the at-sea movements of 48 juvenile southern elephant seals between the ages of 1 and 4 years using locations derived from recorded light levels. There were significant differences in the total amount of the Southern Ocean covered by the different age-groups. The younger seals used a smaller area than the older seals. On average, the younger individuals also made more trips to sea than the older seals and did not travel as far on each trip. Females spent more time at sea than males and there were no significant differences between the total areas used by male and females. In summary,

younger seals remained closer to the island at all times, and they spent more time in more northerly regions than older seals. These differences in behaviour created temporal and spatial segregation between juveniles of different ages. Therefore, I suggest that these temporal and spatial separations help avoid intra-specific competition for resources on land, space on beaches, and at-sea foraging areas. Such modifications of haul-out timing and behaviour enable them to exploit a patchy and unpredictable environment.

Age related shifts in the diet composition of southern elephant seals expands overall foraging niche

## Introduction

The distribution of biological resources within the Southern Ocean is highly variable, unpredictable and patchy at several spatial and temporal scales (El-Sayed 1988; Constable et al. 2003). Spatial and temporal variation in the physical oceanographic factors provide a diversity of habitats that influence the distribution, structure and abundance of ecological communities (Lutjharms 1990; Rodhouse and White 1995; Arrigo et al. 1998; Constable et al. 2003). In recent years our understanding of primary production and energy flow through the lower trophic levels of the marine food web in this region have improved greatly (Arrigo et al. 1998; Constable et al. 2003); however, there is still a significant lack of information regarding energy flow through the mid-order organisms (Rodhouse and White 1995) that are important prey sources for apex predators such as seabirds, pinnipeds and cetaceans. In an environment where food resources may be limited due to intra- and inter-annual variation in productivity and availability of food, it is likely that predator species will display ontogenetic niche shifts that will reduce competition and maximise foraging success for each age class (Van Valen 1965, Takimoto 2003, Chapter 4).

The southern elephant seal (*Mirounga leonina*) is an apex predator of the pelagic open-ocean system. This species has a circumpolar distribution, is a wide-ranging, deep-diving predator that spends more than 80 % of its annual cycle at sea (Le Boeuf and Laws 1994). They are major consumers of biomass, primarily squid and fish (Boyd et al. 1994; Bradshaw et al. 2003; Hindell et al. 2003b). The population of *M. leonina* at Macquarie Island in the Pacific sector of the Southern Ocean has been declining since 1950 for reasons that are still unclear (Hindell et al. 1994), although it has been suggested that this species is susceptible to changes in the availability of prey (Hindell et al. 1994; Guinet et al. 1999; Slip and Burton 1999; McMahon et al. 2003, 2004). In particular, juvenile survival has been suggested to be influenced by ontogenetic changes in morphology, behaviour and foraging experience and appears to be one of the driving factors in the decline and population change in general (McMahon et al. 2003; Hindell et al. 1994).

Recent studies have demonstrated that there is an ontogenetic change in diving and foraging capacity in elephant seals, though their complex physiology is not completely understood; as the animals age and increase in body size, their ability to dive longer and deeper also increases (Le Boeuf et al. 1996; Slip 1997; Stewart 1997; Irvine et al. 2000; Le

Boeuf et al. 2000; Chapter 3; Chapter 4). Elephant seals are also highly sexually dimorphic as adults (although less so as juveniles); however, sex differences in energy use by juveniles relating to the requirements for moulting and sexual development have been demonstrated (Chapter 5). Thus, it is likely that juvenile elephant seals should demonstrate shifts in diet structure as they age toward adulthood.

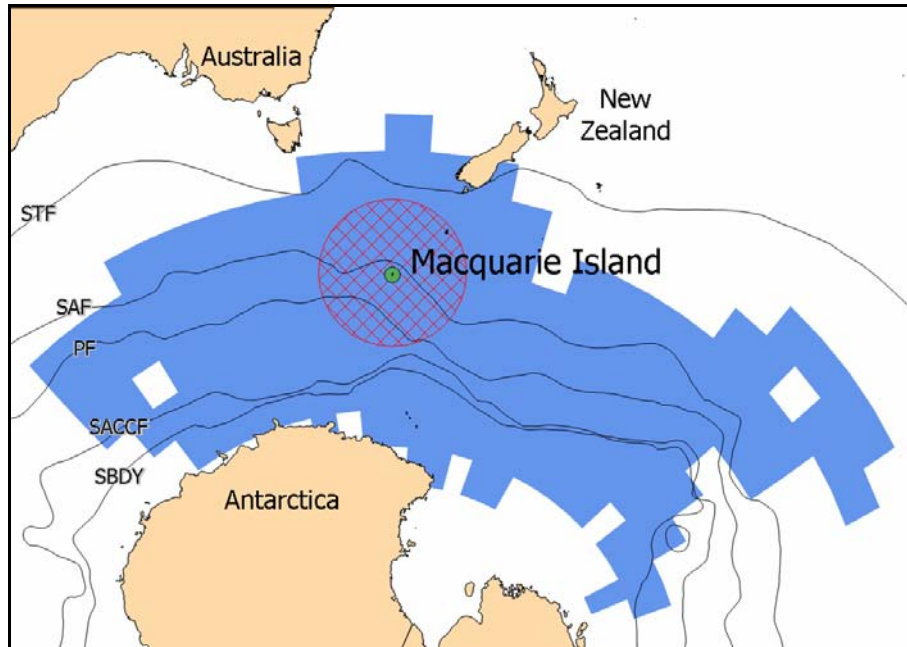
Previous studies of southern elephant seal diet (Rodhouse et al. 1992; Green and Burton 1993; Slip 1995, van den Hoff 2004) have identified that they are opportunistic generalist feeders with a broad foraging niche (Whitehead et al. 2003), with geographical (Green and Burton 1993; Daneri et al. 2000) and seasonal (Piatkowski et al. 2002; Bradshaw et al. 2003) differences in diet composition. However, no one has addressed the hypothesised change in diet composition within the juvenile years.

Therefore, in this study I examine the diet of juvenile southern elephant seals for intra-specific and seasonal differences that may result from variation in at-sea behaviour. Furthermore, I address the complex question of whether the previously observed seasonal differences in metabolic rate within the juvenile age classes are a function of variation in prey species abundance or whether it is variation due to physiological limitations. I hypothesise that 1) because juvenile seals grow and travel farther from Macquarie Island as they age, they may also change their diet composition and size as a function of spatial variation in prey availability; 2) seasonal differences in at-sea behaviour and haul-out patterns may also affect prey availability and hence, diet composition, and; 3) there may be sexual differences in diet selected due to the different metabolic requirements of males and females (Chapter 5). Finally, where intra-specific differences have been found I have calculated the minimum sample required to find a difference using a novel approach that can be used for future lavaging studies.

## Methods

From September 1999 to September 2000, 141 known age juvenile southern elephant seals (McMahon et al. 2003) were stomach lavaged during their annual haul-out periods as they returned ashore at Macquarie Island (158° 57'E, 54° 30'S; Fig. 5.1). Juvenile seals were determined as being between one and four years old, and are referred to as one-, two- or three-year-old seals. Seals caught between the start of September and the end of February

were regarded as having been caught during the summer and March-August representing winter.



*Fig. 5.1. The known foraging range of juvenile southern elephant seals from Macquarie Island, shown as shaded in blue (from Chapter 4), and the possible area the a seal may have used within seven days (700km) of returning to haul-out shaded within the red circle, using 100 km d<sup>-1</sup> as a daily rate of travel (Chapter 4).*

#### *Sample collection*

The beaches on and near the northern isthmus of the island were searched daily for marked individuals returning ashore that day. As the seals returned to the island for either their mid-year (winter) or moult (summer) haul-out, they were caught by placing a canvas bag over the seal's head (McMahon et al. 2000) and anaesthesia administered intravenously using prescribed doses (Chapter 2) of a combined 1:1 mixture of tiletamine and zolazepam (Telazol<sup>®</sup>, Forte Dodge, Castle Hill, NSW, Australia).

Once anaesthetised, the seals were weighed ( $\pm 1$  kg), measured ( $\pm 10$  mm) and lavaged (Slip 1995). The regurgitant was filtered through a 1-mm sieve to retrieve the stomach contents. The lavage procedure was repeated three times to remove the bulk of the stomach contents. The filtered stomach contents were then placed into a storage jar and filled with 70 % ethanol until the contents were sorted and prey items identified.

In preparation for sample sorting and identification, the stomach contents were flushed with fresh water and placed in a sorting tray. From the stomach samples the presence of fish otoliths, eyes and bones, squid mouth parts (consisting of an upper and lower beak), penn and eyes, crustaceans and other invertebrates, parasitic worms, sediment and plastic particles were identified. Lower squid beaks were identified to the lowest taxa possible, using voucher specimen collections (from Malcolm Clarke held at the Australian Antarctic Division) and descriptions in Clarke (1986), and the lower rostral lengths (LRL) measured to  $\pm 0.01$  mm. *Slosarczykovia circumantarcticus* (Cherel 2004) was previously mis-identified as *Brachioteuthis picta* (Rodhouse 1992), *Mastigoteuthis* sp? (Green and Burton 1993) and *Chiroteuthis* sp. (Slip 1995) until correctly identified as a separate genus by Lipinski (2001). Fish otoliths were also identified to genus or species level where possible using a voucher collection (from Dick Williams held at the Australian Antarctic Division) and the descriptions in Williams and McEldowney (1990). Most otoliths showed significant erosion (Williams and McEldowney 1990) and only one pair could be measured.

#### *Statistical analysis - General differences in prey*

To test for overall differences in general prey types (presence/absence) statistical comparisons were made between different sex, age and season groups using ANOSIM analyses on Bray-Curtis dissimilarity matrices (Primer-e, PML, Plymouth, UK) using 999 permutations. Where significant differences between the main effects were found, the differences in prey type (presence/absence) were described using similarity of percentages analyses, SIMPER (Primer-e, PML, Plymouth, UK). This test provided a Global R indicating the discrimination between groups, a significance level of the Global R, the sample statistic, (SSS) and number of permuted statistics (NPS) giving the distribution of the Global R.

#### *Intra-specific differences in prey species abundance*

Common prey species were defined as only those species that were found in > 5 % of samples. Abundance of prey species was defined as the number of beaks within an individual's stomach. To test for intra-specific and seasonal differences in the mean abundance of prey, I used non-parametric multivariate tests (ANOSIMs and SIMPER, as above) that allowed robust analysis of combined prey species data. These tests are limited

in their ability to perform multiple interactions between group variables, so in order to test our main hypothesis (i.e., that there are age differences in the diet of juvenile seals) I needed to control for the potential effects of season and sex. Therefore, based on three *a priori* decisions I used a hierarchical approach (Fig. 5.2), first testing for the effect of sex, then controlling for season and finally for age effects by removing any possible confounding interactions that may occur. Due to the limited number of individual seals lavaged in some of the groups, comparisons were only made where I had more than five individuals in each group and has essentially lead to sex and season effects being treated as random error.

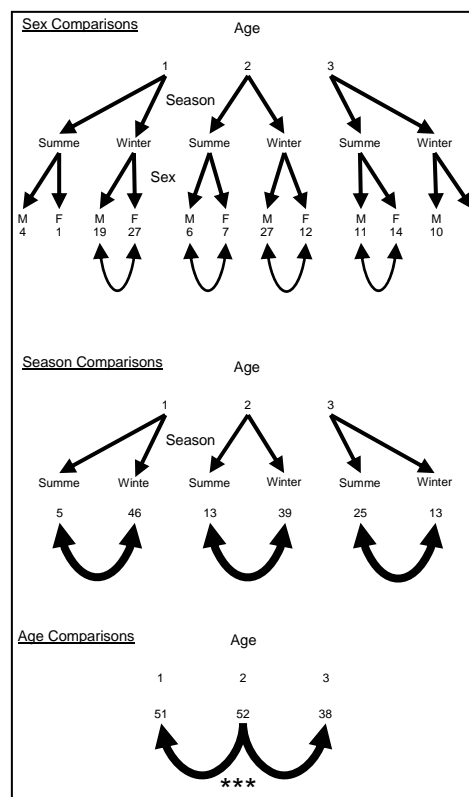


Fig. 5.2. The hierarchal statistical design used in this study to exclude potential confounding effects of sex and season. Comparisons were restricted to groups with >5 stomach samples and are indicated with double-headed arrows. The numbers below each of the tested groups indicate number of samples and the connecting arrows show the tested comparisons. \* - indicates the level of significance ( $P$ ) of each test where (\* > 0.05, \*\* > 0.005 and \*\*\* > 0.001).

### Size of prey

Squid size is known to vary throughout the year. To examine differences in the size of squid eaten by different age and sex groups using two-way general linear models (GLM) and the ANOVA function in the R package (Ihaka and Gentleman, 1996). I compared the mean LRL of the of those common prey species that occurred all age and sex groups and

limited the comparisons to during winter to reduce variation due to size variation of individual squid species.

#### *Minimum sample requirement*

As a guide for future diet studies using stomach lavaging in this species, I determined the minimum number of samples required to detect significant age differences in the abundance of prey in their diet. I reasoned that after a number of samples have been compared for each age group, the addition of further samples will not increase the probability of finding a difference between age groups. I took two samples at random from each age group and compared the groups using an ANOSIM. I repeated this 1000 times, and calculated the number of times that the ANOSIM found a significant difference. I then increased the number of samples taken from each age group by 1 and repeated the process. This was repeated until I reached the maximum number of sample within an age group. I was then able to plot the probability of finding a difference at the 5 % significance level ( $\alpha = 0.05$ ) between age groups against the number of samples required from each age group.

## Results

During their annual moult, as the seals returned in the austral summer, the mean body mass ( $\bar{X} \pm \text{SD}$ ) of juvenile male and female seals ranged from  $200 \pm 42$  kg for one-year olds,  $256 \pm 36$  kg for two-year olds and  $350 \pm 38$  kg for three-year olds. In winter, during their mid-year haul-out each of the age group had increased in mass, where mean masses were  $210 \pm 29$  kg for one-year olds,  $316 \pm 47$  kg for two-year olds and  $438 \pm 92$  kg for three-year olds.

#### *Overall Diet Composition*

Squid remains, frequency of occurrence, were found in all 141 samples (Table 5.1) and fish remains in 107 samples (76 %). Also found in 17% of the stomach samples were remains of *Gammarid* sp. and *Hyperid* sp. amphipods, although these were partially digested and could not be identified further. The occurrence (presence/absence) of squid and fish remains in the overall diet composition was unaffected by seal age and sex, and season (Age: Global R = 0.009, significance level of sample statistic (SSS) = 17.3 %, number of permuted statistics (NPS)  $\leq 0 = 172$ ; Sex: Global R = -0.007, SSS = 85.7 %,

NPS  $\leq 0 = 856$ ; Season: Global R = -0.009, SSS = 63.6 %, NPS  $\leq 0 = 635$ ; Table 5.1).

Also noteworthy was that no plastic particles were found in any of the samples.

*Table 5.1. The frequency of occurrence of overall diet composition from the stomach contents of juvenile southern elephant seals from Macquarie Island, from September 1999 to September 2000.*

	n	Squid remains	Fish remains	Crustacean	worms	sediment
All Seals						
Overall	141	100.0	75.9	17.7	85.8	68.8
Females	64	100.0	79.7	20.3	81.3	64.1
Males	77	100.0	72.7	15.6	89.6	72.7
Summer	43	100.0	76.7	7.0	90.7	37.2
Winter	98	100.0	75.5	22.5	83.7	82.7
1yr						
Overall	51	100.0	82.4	27.5	84.3	78.4
Females	28	100.0	92.9	39.3	85.7	82.1
Summer	1	100.0	100.0	0.0	100.0	100.0
Winter	27	100.0	92.6	40.7	85.2	81.5
Males	23	100.0	69.6	13.0	82.6	73.9
Summer	4	100.0	75.0	25.0	75.0	0.0
Winter	19	100.0	68.4	10.5	84.2	89.5
2yr						
Overall	52	100.0	75.0	17.3	86.5	69.2
Females	19	100.0	73.7	5.3	73.7	57.9
Summer	7	100.0	71.4	0.0	85.7	28.6
Winter	12	100.0	75.0	8.3	66.7	75.0
Males	33	100.0	75.8	24.2	93.9	75.8
Summer	6	100.0	100.0	0.0	100.0	50.0
Winter	27	100.0	70.4	29.6	92.6	81.5
3yr						
Overall	38	100.0	68.4	5.3	86.8	55.3
Females	17	100.0	64.7	5.9	82.4	41.2
Summer	14	100.0	64.3	7.1	85.7	35.7
Winter	3	100.0	66.7	0.0	66.7	66.7
Males	21	100.0	71.4	4.8	90.5	66.7
Summer	11	100.0	81.8	9.1	100.0	45.5
Winter	10	100.0	60.0	0.0	80.0	90.0

### *Squid and fish Taxa*

Fourteen squid and 15 fish taxa were found within the diet samples, excluding combined genera groups where individual species were identified (Table 5.2). The most abundant

squid species found in the samples were *Alluroteuthis antarcticus* (~60 % of samples), *Slosarczykovia circumantarctica* (~68 %) and *Histioteuthis eltaninae* (~80 %). Of the fish taxa identified, two genera of Myctophidae were most common, *Electrona* and *Gymnoscopelus* species, and were found in ~11 and ~9 % of samples, respectively. All taxa are known to have either sub-Antarctic or Antarctic distributions (Clarke 1986; Rodhouse et al. 1992; Slip 1995; van den Hoff 2004).

#### *Prey species abundance differences*

For the number of prey items (abundance) for the different prey species found in an individual's stomach sample, in each of the four comparisons between sexes (controlling for sample size, season and age - Fig. 5.3), there were no significant differences in abundance of prey species between male and female juvenile seals (1-year olds in winter: Global R = 0.069, SSS = 6.2 %, NPS  $\leq 0 = 61$ ; 2-year olds in summer: Global R = 0.064, SSS = 18.8 %, NPS  $\leq 0 = 187$ ; 2-year olds in winter: Global R = 0.077, SSS = 15.2 %, NPS  $\leq 0 = 151$ ; 3-year olds in summer: Global R = -0.008, SSS = 48.4 %, NPS  $\leq 0 = 483$ ). Because there was no sex effect, I pooled the data and tested for a difference between the seasons for each age group. Again, there were no significant seasonal differences within each age group (1-year olds: Global R = 0.102, SSS = 22.4 %, NPS  $\leq 0 = 223$ ; 2-year olds: Global R = -0.014, SSS = 52.0 %, NPS  $\leq 0 = 519$ ; 3-year olds: Global R = 0.054, SSS = 17.6 %, NPS  $\leq 0 = 175$ ). Because there were no sex or season effects, I pooled all our data to determine if there were significant differences in prey abundance between one-, two- and three-year-old seals, which essentially ignores any potential effects of sex and season not found due to reduced statistical power. Our analysis showed that there were significant differences observed between the one-year olds and two- and three-year olds (Global R = 0.148, SSS = 0.1 %, NPS  $\leq 0 = 0$ ; Fig. 5.3). The three most common species in all three age groups (accounting for ~80 % of the diet) were *A. antarcticus*, *S. circumantarctica* and *H. eltaninae*, although they occurred in different proportions (Table 5.3). From the SIMPER analyses, five species accounted for ~70 % of the dissimilarity between one-year-old seals and the two- and three-year olds. These species in order of importance were *H. eltaninae* (> 20 %), *S. circumantarctica* (> 20 %), *A. antarcticus* (> 10 %), the combined lantern fish taxa of *Electrona* sp. (~7 %) and *P. glacialis* (~6 %), whereas one-year-old seals had greater numbers of *S. circumantarctica* and *Electrona* sp., but less *H. eltaninae* and *P. glacialis* than two- and three-year olds.

Table 5.2. The frequency of occurrence (FoO) of squid and fish prey taxa identified from the stomach contents of juvenile southern elephant seals from Macquarie Island. Squid fish species that are found at or south of the Antarctic Polar front are denoted with <sup>a</sup>.

Prey Taxa	FoO (%)	n samples	n beaks	Fish Taxa	FoO (%)	n samples	n otoliths
Squid Taxa							
<i>Alluroteuthis antarcticus</i> <sup>a</sup>	59.86	85	406	<i>Krefflichthys anderssoni</i> <sup>a</sup>	0.70	1	1
<i>Brachioteuthis</i> sp. <sup>a</sup>	38.03	54	90	<i>Protomyctophum choriodon/normani</i>	0.70	1	1
<i>Slosarczykovia circumantarctica</i> <sup>a</sup>	67.61	96	468	<i>Electrona</i> sp. <sup>a</sup> (all sp. combined)	11.27	16	174
<i>Galiteuthis glacialis</i> <sup>a</sup>	25.35	36	54	<i>Electrona carlsbergi</i> <sup>a</sup>	3.52	5	13
<i>Gonatus antarcticus</i> <sup>a</sup>	40.85	58	123	<i>Electrona subaspera</i> <sup>a</sup>	0.70	1	2
<i>Histioteuthis eltaninae</i> (B1)	79.58	113	945	<i>E. carlsbergi</i> / <i>E. subaspera</i>	4.23	6	61
<i>Histioteuthis atlantica</i> (B3)	4.93	7	7	<i>Gymnoscopelus</i> sp. <sup>a</sup> (all sp. combined)	9.86	14	83
<i>Kondakovia longimana</i> <sup>a</sup>	12.68	18	42	<i>Gymnoscopelus bolini</i> <sup>a</sup>	3.52	5	17
<i>Martalia hyadesi</i> <sup>a</sup>	38.03	54	115	<i>Gymnoscopelus braueri</i> <sup>a</sup>	1.41	2	2
<i>Moroteuthis ingens</i> <sup>a</sup>	14.08	20	25	<i>Gymnoscopelus nicholsi</i> <sup>a</sup>	0.70	1	2
<i>Moroteuthis knipovitchi</i> <sup>a</sup>	38.73	55	136	<i>Gymnoscopelus plabilis</i> <sup>a</sup>	0.70	1	4
<i>Moroteuthis</i> sp. <sup>a</sup>	11.27	16	20	<i>Ichthyus australis</i> <sup>a</sup>	3.52	5	5
<i>Philidoteuthis boschmai</i>	1.41	2	2	<i>Paradiplospinus gracilis</i> <sup>a</sup>	0.70	1	1
<i>Psychroteuthis glacialis</i> <sup>a</sup>	34.51	49	191	<i>Bathylagus</i> sp. <sup>a</sup>	0.70	1	1
<i>Taonius pavo</i>	14.08	20	27	<i>Phosichthys argenteus</i>	0.70	1	1
Unidentified species	24.65	35	55	<i>Magnisudis prionosa</i> <sup>a</sup>	0.70	1	3
				<i>Nototheniid</i> type	0.70	1	12
				<i>Dissoistichus eleginoides</i> <sup>a</sup>	0.70	1	2
				<i>Ebinania macquariensis</i> ?	0.70	1	1
				Unidentified species	13.38	19	149
				Unidentified species (probably myctophidae)	18.31	26	949

Table 5.3. The mean abundance and percentage contribution of the common prey taxa in the diet of one- two- and three-year-old southern elephant seals.

Age	1		2		3	
Species	Mean abundance	% Contribution	Mean abundance	% Contribution	Mean abundance	% Contribution
<i>A. antarcticus</i>	3.14	9.3	3.38	17.53	1.84	6.41
<i>Brachioteuthis</i> sp.	0.29	1.11	0.73	3.63	0.97	1.73
<i>S. circumantarcticus</i>	4.67	54.65	3.15	17.67	1.74	3.6
<i>G. glacialis</i>	0.41	1.99	0.38	0.71	0.34	0.35
<i>G. antarcticus</i>	0.47	2.85	1.21	4.29	0.95	1.51
<i>H. eltaninae</i>	2.04	19.73	6.46	44.54	13.29	74.25
<i>K. longimana</i>	0.08	0.01	0.33	0.21	0.55	0.54
<i>M. hyadesi</i>	0.24	0.41	1.02	3.61	1.32	4.12
<i>M. ingens</i>	0.08	0.04	0.17	0.25	0.32	0.39
<i>M. knipovitchi</i>	0.45	1.62	1.23	4.5	1.29	3.34
<i>Moroteuthis</i> sp.	0.2	0.4	0.15	0.1	0.05	0
<i>P. glacialis</i>	0.75	3.19	1.46	2.29	2.03	3.15
<i>T. pavo</i>	0.08	0.03	0.21	0.16	0.32	0.51
<i>Electrona</i> sp.	3.69	3.66	0.81	0.41	0.53	0.03
<i>Gymnoscopelus</i> sp	1.45	0.99	0.38	0.09	0.37	0.07

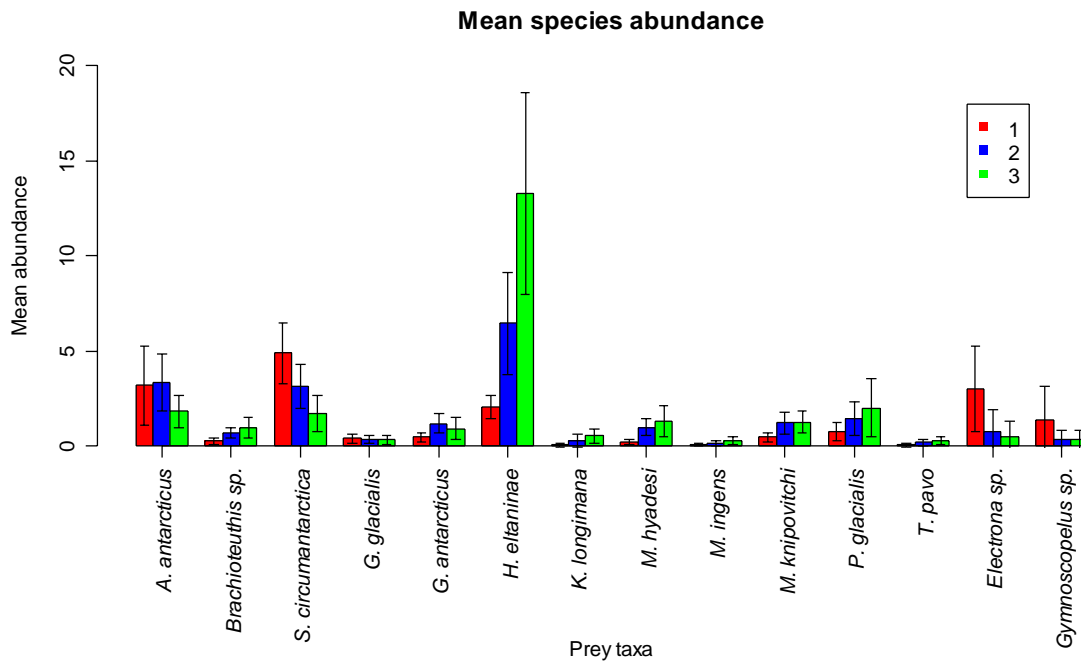


Fig. 5.3. The species abundance ( $\bar{X} \pm 2SE$ ) for the common prey species for one-, two- and three-year-old southern elephant seals from Macquarie Island.

#### Size of squid prey

LRL of the seven squid species found in the diet of all 97 juvenile seals in winter were compared between the three age groups. There were significant differences for only two of the prey species (Fig. 5.4) in the size of beaks found, with older seals taking larger *M. hyadesi* (ANOVA;  $F_{(2,77)}=3.71$ ,  $P=0.029$ ) and *M. knipovitchi* (ANOVA;  $F_{(2,51)}=8.66$ ,  $P<0.001$ ). Sex differences (Fig. 5.5) in size of prey between male and female seals were found for only one prey species, *M. hyadesi*, where males had larger beaks in their samples (ANOVA;  $F_{(1,77)}=4.64$ ,  $P=0.034$ ).

#### Minimum sample required

There was a clear asymptote in the curve for the number of samples needed to find a significant difference (randomised ANOSIM; Fig. 5.6). After including 13 random samples from each age group the probability of finding a difference ( $SSS < 0.05$ ) between the groups was 95 %. By comparing 15 samples there was a 99 % probability of finding a significant difference.

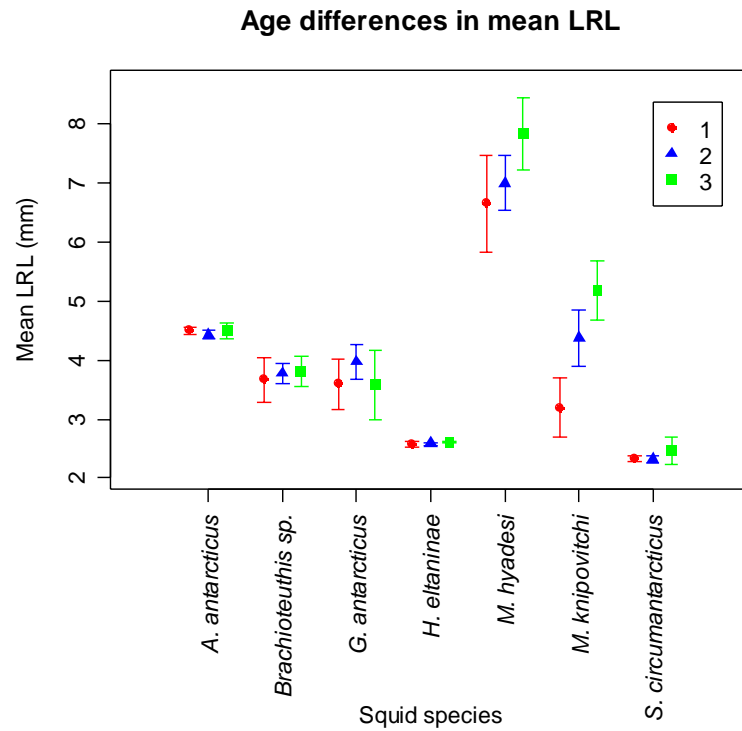


Fig. 5.4. Differences in LRL ( $\bar{X} \pm 2SE$ ) for the common squid species found in the stomachs of one-, two- and three-year-old southern elephant seals from Macquarie Island.

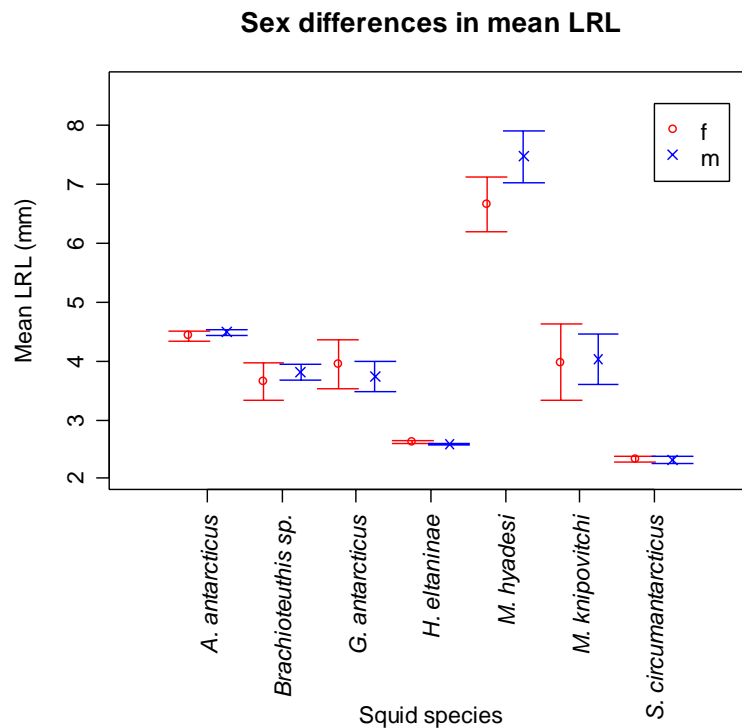


Fig. 5.5. Differences in LRL ( $\bar{X} \pm 2SE$ ) for the common squid species found in the stomachs of male and female southern elephant seals from Macquarie Island.

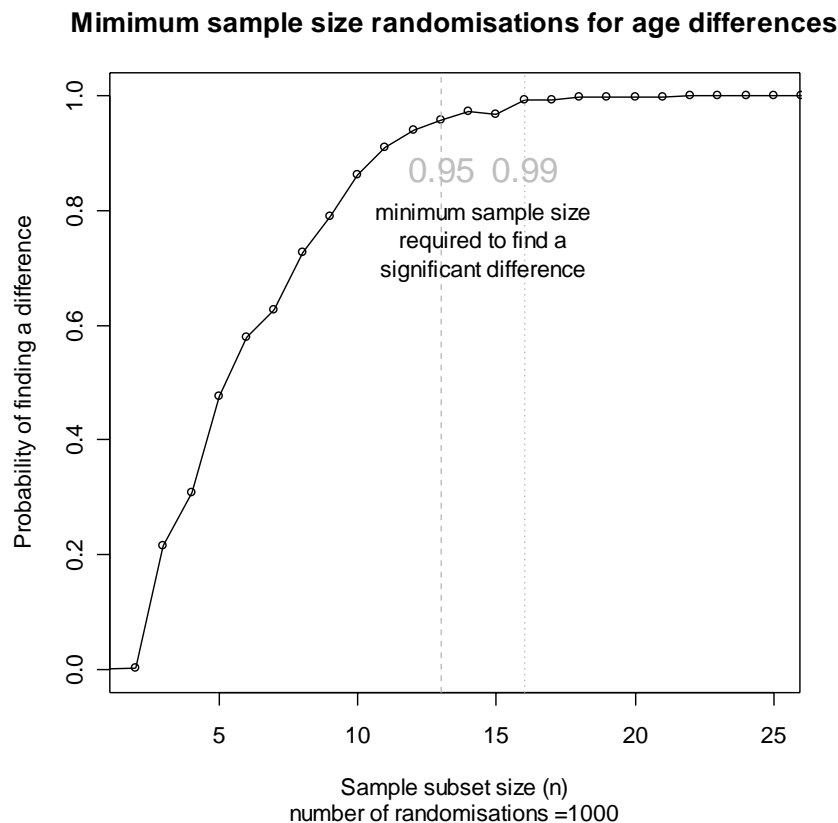


Fig. 5.6. The minimum number of samples required to find a significant difference ( $P > 0.05$  and  $> 0.01$ ) between one-, two- and three-year-old southern elephant seals using a randomised selection of samples from our data.

## Discussion

Southern elephant seals are deep diving generalist feeders opportunistically eating whatever is large enough that they find while foraging, and this particular foraging strategy may have evolved as a result of the dynamic and unpredictable seasonal and spatial distribution and abundance of target prey within the Southern Ocean. This species shows a high degree of dimorphism with adult females and males being at least ten and 100 times greater in mass than newborns. Assuming that resources are limited, however, one might expect that behavioural shifts among different ‘ecological species’, or sub-groups within the species would lead to a reduction in intra-specific competition for food resources (Polis 1984; Bolnick et al. 2003; Takimoto 2003; Chapter 4). There are clear differences in diet between the one-, two- and three-year-old seals, in terms of both species abundance and prey size, but with no sex or season effect. Though it is noteworthy that no sex or season effects were found this may have alternatively been due to decreased statistical power for these analyses and could potentially increase the random error within the tests for age

differences. Nonetheless, the lack of a sex effect indicates that these dietary changes are not primarily driven by differing metabolic requirements between the sexes (Chapter 5). Rather, dietary changes appear to be a function of ontogenetic changes in foraging capacity and range, regulated by physiological limitations and seasonal haul-out patterns (Chapter 4).

As with many other species (Adams 1996; Wikelski and Wrege 2000; Spina 2000) an increase in size with age, influences the ability of an individual to obtain prey and expand its foraging niche (Polis 1984; Radloff and Du Toit 2004). As seals grow there are changes in the physiological diving abilities which allow older, larger individuals to dive deeper and longer (Le Boeuf et al. 1996; Burns 1999; Hindell et al. 1999; Irvine et al. 2000). Thus, older individuals that can remain at deeper depths for a longer period have greater access to deeper-dwelling species. Our results show a clear change in the composition of diet between juvenile seals. The older seals have greater proportions of the larger squid in their samples (*K. longimana*, *M. hyadesi*, *M. ingens*, and *M. knipovitchi*) which may not have been available to smaller individuals. Indeed, there is some evidence for pelagic cephalopods that older and larger individuals are capable of more extensive vertical migrations (Jackson 1993; Arkhipkin and Bjørke 1999).

There was, however, no difference in the size of most other prey species ingested. Therefore, differences in prey composition between age groups could also be due to variation in foraging range that appears to be regulated, in part, by variation in seasonal haul-out patterns according to age (Chapter 4). This regulation appears to occur independently of dispersal capacity because different age classes demonstrate similar rates of travel (Chapter 4). Although our results only represent the diet as the seals return to the island, it appears that variation in foraging and haul-out behaviour in conjunction with modification of diet composition all contribute to a general reduction in intra-specific competition for this wide-ranging Antarctic marine predator.

Other studies of elephant seal diet have shown differences between juveniles and adults (Green and Burton 1993; Slip 1995), although the nature of these differences were inconsistent. Slip (1995) found that juveniles were different from both male and female adults, while Green and Burton (1993) found only differences between juveniles and adult

females that could not be readily explained. Only one other study has specifically tested for differences among size/age classes, but results were inconsistent and no trends found (Rodhouse et al. 1992).

Three species dominated the diet, although there were distinct differences between the different age groups. The diet of one-year-old seals was dominated by *S. circumantarcticus*, a muscular squid with a broad Southern Ocean distribution (Cherel et al. 2004). In contrast, the two- and three-year olds' diets were dominated by the *H. eltaninae* which has a sub-Antarctic distribution (Cherel et al. 2004). Furthermore, the diet of two-year olds, though not statistically significantly different from that of three year olds, was intermediate between the younger and older seals. All common prey species were found in all age groups, therefore, it seems likely that all prey species are encountered by the different age groups but with differences in availability. Availability could be influenced by whether they are a solitary or schooling species, or by the relative costs of catching prey (for example, a slow swimming species versus a cryptic fast swimming species). For both of the larger squid species commonly found in the diet of the different age groups in winter, *M. knipovitchi* and *M. hyadesi*, the size of prey also increased with age that may only allow larger seals, able to forage deeper are able to catch these larger prey, thus increasing the range of prey sizes available and their foraging niche (Jackson et al. 2004; Radloff and Du Toit 2004).

There is a suite of methods available for the determination of diet, including direct and indirect observation, genetic sampling (Symondson 2002, Jarman et al. 2002), fatty acid signature analyses (Brown et al. 1999; Bradshaw et al. 2003; Iverson et al. 2004), stable isotope analyses (Iverson et al. 2004; Hooker et al. 2001), and the study of remains in faecal and stomach contents (Santos et al. 2001). All these methods have advantages and disadvantages; but it is only through the direct analysis of prey remains, that we can determine both species' identity and ecological information (such as size structure) about the prey. Furthermore, our use of a novel approach to determine the minimum sample required to find a difference has given greater confidence to our results and provides some guidance for future preliminary studies for any species using this technique to minimise disturbance and the impact of dietary studies.

In this study I lavaged the stomachs of the seals as soon after their return as possible; however, these samples are only representative of their foraging as they return to Macquarie Island (Fig. 5.1) and not their entire foraging areas. Elephant seals have a rapid rate of digestion (~13 h; Krockenberger and Bryden 1994), although prey hard parts may be retained in the stomach for over 7 days (Tollit et al. 1997). Therefore, our samples are likely to have come from within 700km of the island, using 100 km d<sup>-1</sup> as the rate of travel by juvenile seals (Chapter 4) being a conservative maximum range for potential prey items to have been consumed. This range reflected the reduced abundance of Antarctic species in their diets. The results may also over-estimate the presence of prey with larger hard parts due to differential digestive rates (Daneri & Carlini, 2002). Furthermore, some of the prey remains in our samples may have been from secondary ingestion (Arnett and Whelan 2001). From the few diet studies of squid found in the Southern Ocean (Phillips et al. 2003) it is clear that they are voracious predators that eat fish and squid and show seasonal differences in diet.

Squid and fish, including some commercially taken species (Burton and van den Hoff 2002), are the main prey of southern elephant seals (Rodhouse et al. 1992; Green and Burton 1993; Slip 1995; Daneri et al. 2000; Piatkowski et al. 2002; Bradshaw et al. 2003; van den Hoff et al. 2003; van den Hoff 2004) although the variation in their relative proportions is less well-known (Santos et al. 2001) for ecological and methodological reasons (Bradshaw et al. 2003). As in other diet studies of Macquarie Island juvenile elephant seals (Green and Burton 1993; van den Hoff 2004), squid are the primary prey, however, the occurrence of fish remains found in our study (all age groups ~76 %) were higher than in previous studies where fish were found in only 10 % of samples (Green and Burton 1993). This difference is likely to be due to inter-annual variability in the availability of fish prey as suggested by Daneri et al. (2000).

Compared to previous studies (Green and Burton 1993; van den Hoff 2004), the fish component of our juvenile diet sample contained many more fish species from pelagic, demersal and benthic habitats, including the Patagonian Toothfish (*Dissostichus eleginoides*) and *Echinania macquariensis*, an endemic benthic species only found around Macquarie Island (Williams 1988). The main difference, however, is the dominance of the squid, *S. circumantarcticus*, which contributed ~55 % of the total number of beaks in our

samples, but only ~6 % in Green and Burton (1993). Other differences include a reduction in *H. eltaninae* (~12 % compared to ~20 % in our study) and *A. antarcticus* and *M. knipovitchi* (~30 and 12 %, respectively compared to (9 and 1.6 %, respectively in our study). These species are all commonly found south of the Polar Front (except *H. eltaninae*); therefore, these differences may result from a change in prey species availability among years due to inter-annual variation in the position or strength of water mixing at the Polar Front (Antonelis et al. 1994).

Although our data only represent the end of the foraging trip, there were clear age-related differences in diet, though it still remains unclear as to the proportions of fish and squid that are eaten while farther away at sea. As the stomach contents are likely to have been collected in broadly similar geographic regions (and there was no evidence of season changes in diet composition), these differences must relate to some intrinsic difference in the seals (i.e., size; Radloff and Du Toit 2004). The intra-specific differences in diet composition linked with the increased foraging ranges with age (Chapters 3 and 4) provide further evidence to support the hypothesis that ontogenetic niche expansion acts to reduce intra-specific competition. However, the diet composition varies with age and spatially, which needs to be addressed using the suite of dietary tools currently available to gain a better understanding of the dynamic ecological niche of this apex predator.

## Summary

Southern elephant seals are important apex predators in a highly variable and unpredictable marine environment. In the presence of resource limitation, foraging behaviours evolve to reduce intra-specific competition increasing a species' overall probability of successful foraging. I examined the diet of 141 (aged 1-3 years) juvenile southern elephant seals to test the hypotheses that differences between ages, sexes and seasons in diet structure occurred. I describe prey species composition for common squid and fish species and the mean size of cephalopod prey items for these age groups. Three cephalopod species dominated the stomach samples, *Alluroteuthis antarcticus*, *Histeoteuthis eltaninae* and *Slosarczyzhkovia circumantarcticis*. I found age-related differences in both species composition and size of larger prey species that probably relate to ontogenetic changes in diving ability and haul-out behaviour and prey availability. These changes in foraging

behaviour and diet are hypothesised to reduce intra-specific food competition concomitant with the increase in foraging niche of growing juveniles.



### Juvenile southern elephant seals exhibit seasonal differences in energetic requirements and use of lipids and protein stores

In press as: Field IC, Bradshaw CJA, Burton HR, Hindell MA (2005) Patterns of onshore mass change and metabolism in juvenile southern elephant seals. *Physiol Biochem Zool* 78(4):491-504

## Introduction

Physiological flexibility allows long-lived individuals to adapt to changes in energetic requirements throughout their lifetime and, generally, juveniles demonstrate the greatest flexibility in metabolic rates and pathways (Robbins 1993; Post and Parkinson 2001). Nonetheless, there is a paucity of research on intra-specific differences in metabolic rates (Nagy 2000). Though in general the energetics of marine mammals has been studied extensively (reviewed in Costa and Williams 1999; Boyd 2002) juveniles in the wild have not been the direct focus of attention, a group where body size has been shown to influence future reproductive success and thermoregulatory capacity (Le Boeuf and Reiter 1988; Clinton and Le Boeuf 1993, Hansen et al. 1995). Furthermore, the evidence suggests that juveniles have the greatest energetic demands, for growth, as they develop toward maturity (Costa and Williams 1999; Boyd 2002). As such, in capital-breeding marine mammals it has been hypothesized that there should be differences in energy management between the sexes during maturation.

Southern elephant seals (*Mirounga leonina*) are one of the most morphologically and physiologically extreme mammal species. They are highly adapted for a marine existence and spend more than 80 % of their annual cycle far from land while foraging for deep-dwelling prey (< 200 m). They also demonstrate some of the longest fasting periods of any pinniped while on land (Le Boeuf and Laws 1994). Southern elephant seals have a circumpolar distribution throughout the Southern Ocean, are wide-ranging (capable of travelling in excess of 5000 km from their breeding and moulting areas - Hindell and McMahon, 2000), dive to extreme depths (> 1500 m - Hindell 2002) and are important apex predators that consume large quantities of prey to maintain and provision themselves for successful breeding (Knox 1994; Boyd et al. 1994; Hindell et al. 2003).

The Macquarie Island population of southern elephant seals (~ 80 000 individuals), representing approximately 10 % of the species' total abundance (Le Boeuf and Laws 1994, McMahon 2003), has been declining since the 1950s (Hindell 1991; McMahon et al. 2003; McMahon et al. 2004). The most plausible ultimate cause of the decline is food limitation (Hindell 1991; McMahon et al. 2003; McMahon et al. 2004). A recent long-term demographic study of the Macquarie and Marion Islands populations by McMahon (2003) demonstrated that for the Macquarie Island population changes in juvenile survival (1-4

years) affected the rate of population change more than other demographic parameters (e.g., adult survival and fecundity). Therefore, it appears that juvenile survival to reproductive age is closely related to the ability of juveniles to find and assimilate food resources and to allocate these energy reserves to growth and eventual reproduction.

Most metabolic and physiological studies have focused on adults when ashore or at sea (Boyd et al. 1993; Slip et al. 1994, Boyd et al. 1999; Hindell et al. 2000), or on the interactions between mothers and pups (Arnbom et al. 1993; Hindell and Slip 1997; Biuw 2003), with little attention given to the ontogeny of metabolic changes after the first year of life (Hindell and Burton, 1987). As seals grow, an increase in absolute metabolic rate is expected due to the increasing body size, but there is also likely to be an increased demand for somatic growth. There may also be reductions in overall metabolic requirements due to increased efficiency in foraging behaviour, energy assimilation and use (Schmidt-Neilsen 1997). Also, a number of studies have shown that body composition (the amount of lipid and protein stores that are available for catabolism) is important in the use of energy reserves where seals with greater amount of lipids will preferentially catabolize lipids. Elephant seals, like most mammals, use lipid reserves for energy, sparing protein while fasting (Houser and Costa 2001; Noren et al. 2003) but also need to retain lipids (fat sparing) as a component of blubber required for thermoregulation (Worthy and Lavigne 1987), buoyancy and hydrodynamic streamlining (Webb et al. 1998; Biuw et al. 2003).

As seals grow there may be significant differences between the sexes in both the amount of energy used and the tissue source from which it is derived given that females demonstrate earlier sexual development relative to male peers (McMahon et al. 1997; Boness et al. 2002, McMahon 2003). Precocious development appears to aid primiparous females (Siervogel et al. 2003) due to earlier lactation requirements (~ 3 to 4 years old - McMahon et al. 2003), while males continue greater somatic growth until reaching maturity later (~ 8 to 10 years - McCann 1980) to increase reproductive potential by maximizing body size necessary for extreme male-male competition. Therefore, precocious development should result in females having a tendency to spare lipid and burn more protein when compared to same-age males.

The timing of terrestrial haul-outs also changes with age (Carrick et al. 1962; Hindell and Burton, 1988; Kirkman et al. 2001; Wheatley, 2001; Chapter 4). After juveniles go to sea following their annual moult (~32 days ~Dec-Jan), they return to land during the winter (~24 days ~ Apr-Aug). The function of this winter, or ‘mid-year’, haul-out is unclear, but it may be due to physiological restrictions, development, parasite reduction, social interactions, reduction of intra-specific competition or simply to rest (Carrick et al. 1962; Condy 1979; Ling and Bryden 1981; Burton 1985; Neumann 1999; Chapter 4). The moulting and mid-year haul-outs clearly serve different functions, and it is likely that juvenile seals expend more energy during the moult due to the elevated energetic demands associated with the production of new epidermis and hair and increased rates of heat loss. Regardless of the function of the mid-year haul-out, if we assume that it is the same for all juveniles, then differences in metabolic rate between the sexes may be due to developmental differences. These differences may also be apparent between haul-out periods when females might reduce metabolic rates to conserve energy reserves for growth, maintenance and provisioning for breeding and fasting.

In this paper I test the hypothesis that during the juvenile years (1 to 3 years), metabolic rate changes in response to differences in the way energy is stored and used as a function of growth and development, and that these patterns are also influenced by the function of the specific terrestrial haul-outs (i.e., mid-year or moult). Specifically, I examine changes in (1) rates of mass loss, (2) changes in body composition and (3) energy use among different age groups, sexes and haul-out periods (moult and mid-year). Observed trends are discussed in terms of the proportions of lipid and protein used to derive the energy needed during a fast. I predict that due to precocious development, females will have reduced metabolic rates to those of similar-aged males that allow females to conserve energy and increase fecundity.

## Methods

Between November 1999 and February 2001, 55 juvenile southern elephant seals were captured as part of a long-term demographic study of the population on Macquarie Island (Hindell et al. 1994a; McMahon et al. 2003). Data for this study were collected with Australian Antarctic Animal Ethics Committee approval (ASAC 2265 and 1171) and with Tasmanian Parks and Wildlife Service permits. Seals were caught and immobilized as they

returned for their moult and mid-year haul-outs, and then again at the end of the haul-outs before returning to sea. Seals ranged in age from 13- to 33-months at the time of capture and were subsequently allocated into one- and two-year-old age groups.

Seals were caught by hand by placing a canvas bag over the seal's head (McMahon et al. 2000), anaesthesia was administered intravenously and using prescribed doses (Chapter 2) of a combined 1:1 mixture of tiletamine and zolazepam (Telazol<sup>®</sup>, Forte Dodge, Castle Hill, NSW, Australia). Once anaesthetized the seals were weighed using a digital scale ( $\pm 1$  kg; Dillon ED-2000, Salter Weigh-Tronix Pty Ltd., Victoria, Australia) and measured ( $\pm 1$  cm). Serial length and girth measurements were made to calculate total body volume (Gales and Burton 1987). Morphometric measurements were made across seven sections (Fig. 6.1), with the head and hips to the base of the tail forming cones and the rest of the body sections forming truncated cones (Chapter 2). Measures of blubber thickness were obtained corresponding with the girth measurements along the seal's dorsal side using an ultrasound backfat depth system (A-Scan Plus<sup>™</sup>, Sis-Pro Inc., Woodbury, MN, USA). From these morphometric and ultrasonic measurements, total blubber and lean tissue volumes were calculated. It should be noted that this method, though valid (Gales and Burton, 1987, Slip et al. 1992, Worthy et al. 1992, Webb et al. 1998, Mellish et al. 2004) has been shown in some other species to have discrepancies with other techniques and absolute values of protein use may be overestimated (Worthy and Lavigne 1983); however, in a relative study such as ours with equal variability across sample groups, this method is valid for within-sample comparisons.

This method assumed that individuals were circular in cross-section, such that the diameter for any cross-section was equivalent to the circumference divided by  $\pi$ . I also assumed that all the blubber lies in the hypodermis and over the whole body and that the flippers contain insignificant amounts of subcutaneous fat (Chapter 2). Total blubber mass (Slip et al. 1992b; Webb et al. 1998) was calculated by multiplying the blubber volume by the density of blubber, taken as  $0.95 \text{ g cm}^{-3}$  (Gales and Burton 1987). Some past studies (Slip et al. 1992; Webb et al. 1998) measured 18 blubber depths where as I have only measured six. To address the variability between using 6 versus 18 blubber depth measurements for calculating adipose tissue volume, I used data from 311 other seals for which I had taken 18 ultrasound measurements (these seals were not sampled longitudinally and were

therefore not included in this study). I used linear regression to model variability between lean volumes calculated using 6 (Vol6) and 18 (Vol18) ultrasound measurements. I found a strong positive relationship ( $\text{Vol18} = 1.0144 \cdot \text{Vol6} + 0.0036$ ;  $r^2 = 0.999$ ). Although the slope of this relationship was close to 1.0, I used this (1.0144) as a correction factor in calculating adipose tissue volume (Fig. 6.2). This technique has shown strong agreement with isotopic techniques in the calculation of body composition (Webb et al. 1998) with mean error being  $0.01 \pm 4.25\%$  and *in situ* measurements of blubber depth (Mellish et al. 2004). Lean body mass was calculated by subtracting the blubber mass from the total body mass.

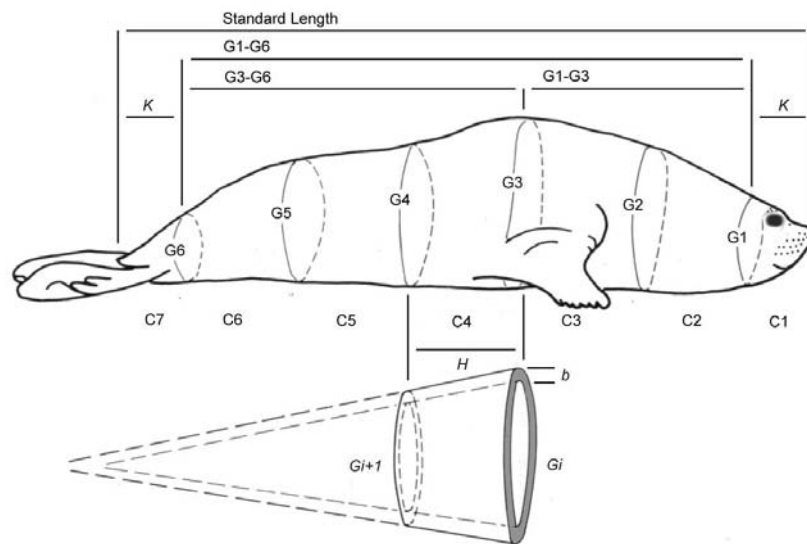


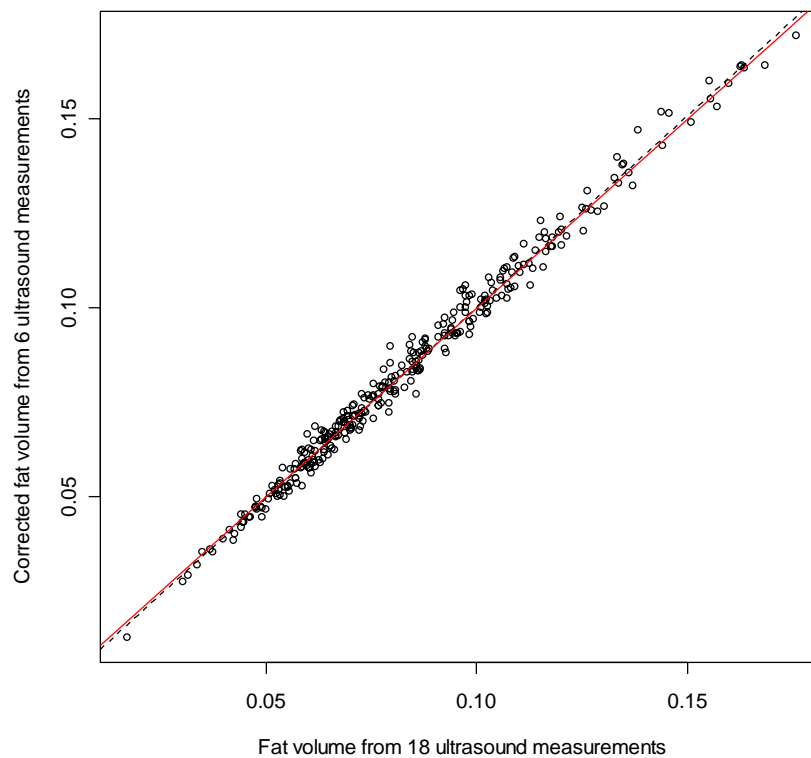
Fig. 6.1. Morphometric measurements used in the calculation of a blubber volume. G1 to G6 represent the circumference of the body at sites 1 to 6, thus creating 7 cones (5 truncated and 2 terminal cones). The depth of blubber ( $b$ ) was assessed at the dorsal surface of all 6 sites and used to calculate total blubber volume (after Chapter 2).

#### *Indices of body composition*

The following assumptions were made to convert measurements into the amounts of fat and protein present: (i) all lipids metabolized by the seals were accounted for by the changes in total blubber mass, which contains 95 % of the dissectible fat (Bryden, 1967), and any protein metabolized was derived from changes in total lean mass; (ii) energy densities of pure fat and protein are  $39.5 \text{ MJ kg}^{-1}$  and  $17.99 \text{ MJ kg}^{-1}$ , respectively (Schmidt-Nielsen, 1975, Reilly and Fedak, 1990); (iii) lean tissue consists of 27 % protein and 73 % water (Pace and Rathbun, 1945; Slip et al. 1992b); and (iv) the animal's state of hydration remains constant over the fasting period (Ortiz et al. 1975). Thus,

$$\text{Energy Expenditure} = \text{BML} * E_{\text{lipid}} + \text{LML} * k_{\text{lean}} * E_{\text{lean}}$$

where BML = blubber mass loss, LML = lean mass loss,  $E_{\text{lipid}}$  = energy provided from lipid mass loss ( $39.5 \text{ MJ kg}^{-1}$ ),  $k_{\text{lean}}$  = proportion of lean mass that is protein (0.27),  $E_{\text{lean}}$  = energy provided from protein mass loss ( $17.99 \text{ MJ kg}^{-1}$ ).

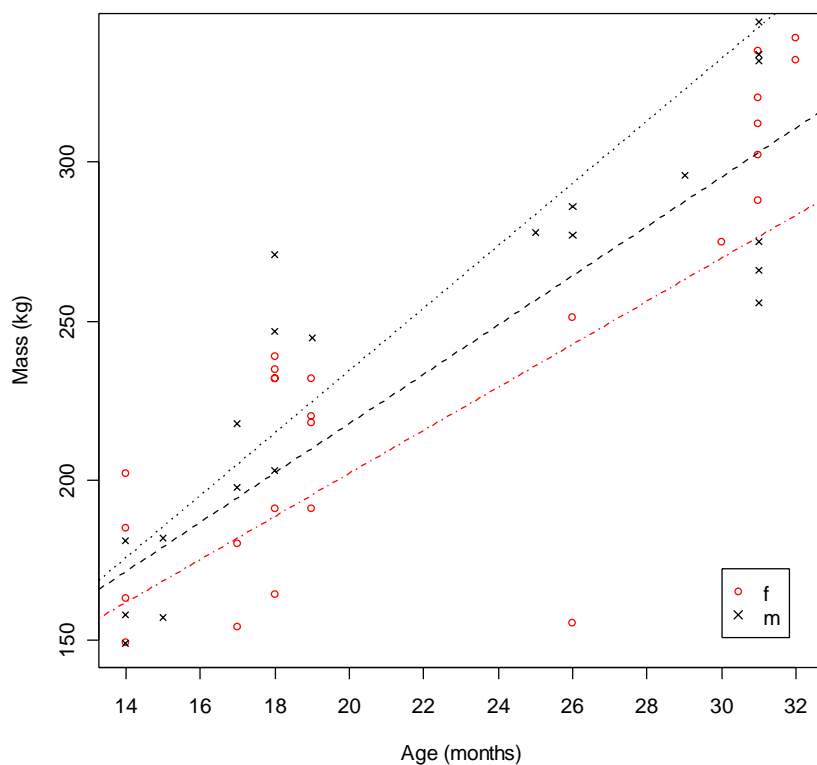


*Fig. 6.2. The relationship between volume of fat calculated using 18 ultrasound measurements and corrected volume using 6 ultrasound measurements, showing the ‘best fit’ linear regression line (dotted line;  $r^2=0.989$ ) and reference line (solid line;  $y = x$ ).*

Body size is fundamental in determining metabolic rate by standard allometry (Kleiber 1975; Schmidt-Nielsen 1997) where there is an intra-specific increase in body mass with age ( $r^2=0.773$ ; Fig. 6.3). Therefore, to remove variability due to the size of the individual I used mass as a covariate in our analyses. To describe the overall changes in body composition I chose to compare overall mass loss, lean-tissue loss and adipose-tissue loss. Before any comparison of energy use could be made, I determined if the seals had similar proportions of adipose to lean tissue at the start and end of a haul-out to determine if all juveniles had similar energy reserves available to them. Differences in body composition

between the start and end of a haul-out were used to measure the daily total energy expended. To examine if seals differed in the relative amount of energy derived from various body components, I also calculated the proportion of total energy derived from lipids in their fat stores.

In addition to the availability of specific substrates, there are limited amounts of body lipid and protein that can be used for energy production without causing acute loss of tissue (i.e., the breakdown of organ tissue or reduction in heat insulation - Cahill 1979; Cherel 1987; Reilly 1989). Therefore, I calculated the end lean mass as a proportion of lean mass at the start of a haul-out to investigate to what degree individuals engage in protein metabolism during the course of the haul-out fast. I also calculated adipose-tissue mass as a proportion of body mass at the end of a haul-out to examine whether individuals retain enough fat for energy reserves and thermoregulation (Cahill 1979; Fedak et al. 1996; McConnell et al. 2002; Biuw 2003).



*Fig. 6.3. Change in mass for one- and two-year-old juvenile elephant seals with age in months, showing the 'best fit' linear regression lines (dashed line for model includes age, sex and an age\*sex interaction ( $r^2=0.773$ ), dotted line for males ( $r^2=0.66$ ) and dot-dash line for females ( $r^2=0.636$ )).*

*Statistical analysis*

I compared one- and two-year-old seals, sexes and the two haul-outs using general factorial generalized linear models (GLM) in the R package (Ver. 1.8.1, Ihaka and Gentleman 1996) including body mass as a covariate for the different response variables. Other studies have shown energetic differences in seasonal requirements and energy use (Boyd et al. 1993; Hindell et al. 1994b), and between sexes (Beck et al. 2003a) and age and size of seals (Burns 1998). Therefore the models tested for the effect of main factors (e.g., age, sex and haul-out) and all two-way interactions and three-way interactions with mass on the response variables. Examination of the residuals for all models indicated that a Gaussian family error distribution with a log-link were the most appropriate model structures for the input data.

There was no *a priori* reason to assume a single model to describe the contribution of terms and their interactions to the response variables, so I used a form of model selection with sample-size-corrected Akaike's Information Criteria (AICc) to select the most-parsimonious model(s) (Lebreton et al. 1992; Burnham and Anderson 1998). AICc is calculated as:

$$\text{AICc} = \text{LL} + 2K + \frac{2K(K+1)}{(n-K-1)}$$

where LL = -2 log-likelihood calculated from the mean squared error and the Type III sum of squares error for each general factorial GLM,  $K$  = the number of model parameters and  $n$  = sample size. AICc values are then ranked on a relative scale from 0 (poor) to 1 (good) (i.e., model weight, Burnham and Anderson 1998). Thus, 'best-fit' model(s) have the lowest AICc value and the highest model weight (Lebreton et al. 1992). To test between the most-parsimonious models, only the top models when summed contributed to greater than 0.5 of the total AICc model weights were considered. To determine the effect of any term seen to be significant in selected models I used a  $\chi^2$  analysis of deviance. The result of this model selection are shown as the ranked, most-parsimonious models, their individual AICc weight, the significance terms of each model and specific-term tests using analysis of deviance. Finally, from these models I used a predictive model averaging procedure to determine the magnitude of the effect of the significant terms, keeping all

other dependent variables constant (Burnham and Anderson 1998). Here, the coefficients for significant terms in the top competing models were modified by their AICc weights and averaged over all models considered to provide model-averaged response predictions.

## Results

The overall average mass loss per day for the moult and mid-year haul-outs were  $2.1 \pm 0.5$  and  $2.2 \pm 0.6$  kg d<sup>-1</sup> over  $32.2 \pm 5.6$  and  $24 \pm 3.6$  days, respectively. Moulting individuals were younger and smaller than those in the mid-year because they were caught earlier in the year. There were differences between haul-outs, ages and sex in all mass-loss parameters (Table 6.1) and in the amounts and metabolic sources of energy (Table 6.2) used by the different age groups and sexes that are described below.

### *Overall mass loss rate*

There were significant differences in the overall mass loss rate in the different haul-outs and a positive relationship with body mass. The candidate models from our model selection showed strong *mass* and *haul-out* effects which were both significant in our analysis of deviance (*mass*,  $\chi^2_1 = 71.665$ ;  $P < 0.001$ ; *haul-out*,  $\chi^2_1 = 0.694$ ;  $P = 0.021$ ; Table 6.3). From our predictive model averaging using all contributing models and keeping *mass*, *sex* and *age* constant, the overall mass loss rate was 12.6 % higher on average in the moult than in the mid-year haul-out.

### *Lean-tissue loss rate*

For the rate of lean-tissue loss there were significant differences between sexes and haul-outs and a positive relationship with mass. The candidate models showed strong *mass*, *sex* and *haul-out* effects which were all significant in our analysis of deviance (*mass*,  $\chi^2_1 = 17.222$ ;  $P < 0.001$ ; *sex*,  $\chi^2_1 = 5.064$ ;  $P = 0.029$ ; *haul-out*,  $\chi^2_1 = 5.140$ ;  $P = 0.028$ ; Table 6.3). From our predictive model averaging using all contributing models, keeping all dependent variables constant except *haul-out*, in the moult lean-tissue loss rate was 31.2 % higher on average than in the mid-year haul-out. Also, there was a significant difference between the sexes, thus keeping all dependent variables in the model averaging constant except for *sex*, females used on average 15.1 % more lean-tissue than males of similar size and age during the same haul-out.

*Table 1. Age and sex differences in mass loss for juvenile southern elephant seals in their two annual haul-outs including proportion of fat and lean mass at the start and end of the moult and mid-year haul-outs, reported as means with SD below.*

Haul-out	Age	Sex	Days	Mass (kg)	End mass (kg)	Mass loss rate (kg <sup>-1</sup> d <sup>-1</sup> )	Lean mass (kg)	End lean mass (kg)	Lean mass loss rate (kg <sup>-1</sup> d <sup>-1</sup> )	Fat mass (kg)	End fat mass (kg)	Fat mass loss rate (kg <sup>-1</sup> d <sup>-1</sup> )	Ratio of fat:lean	End ratio of fat:lean
Moult	1	F (4)	31.75	174.75	119.50	1.75	126.76	99.26	0.87	47.99	20.24	0.88	0.38	0.20
			2.63	23.44	17.06	0.22	18.05	14.07	0.15	5.59	3.00	0.07	0.02	0.00
		M (5)	25.40	165.40	123.60	1.66	119.30	103.78	0.61	46.10	19.82	1.05	0.39	0.19
	2	F (2)	4.28	15.11	4.22	0.44	9.29	3.71	0.28	6.46	2.98	0.19	0.03	0.03
			32.00	203.00	133.50	2.15	149.74	109.74	1.23	53.26	23.76	0.92	0.36	0.22
		M (3)	8.49	67.88	44.55	0.16	50.92	36.59	0.12	16.96	7.96	0.04	0.01	0.00
Mid-year	1	F (12)	33.33	280.33	200.33	2.40	204.42	167.55	1.11	75.91	32.78	1.29	0.37	0.20
			0.58	4.93	7.77	0.27	4.11	2.71	0.16	7.89	5.80	0.18	0.04	0.03
		(14)	29.86	198.07	140.29	1.91	144.02	117.01	0.88	54.05	23.28	1.03	0.38	0.20
	2	F (8)	5.01	51.95	36.25	0.42	38.44	30.26	0.31	14.06	6.57	0.21	0.03	0.02
			22.75	207.33	169.17	1.68	141.53	128.34	0.58	65.80	40.82	1.10	0.47	0.32
		M (6)	2.18	29.96	26.31	0.26	21.09	18.89	0.29	9.89	9.16	0.25	0.04	0.05
Mid-year	1	F (12)	23.50	230.33	186.33	1.88	157.77	143.99	0.59	72.57	42.34	1.30	0.46	0.30
			2.74	28.61	34.29	0.39	22.82	28.40	0.50	6.58	7.60	0.25	0.04	0.04
		(15)	22.88	312.88	263.88	2.15	218.06	194.38	1.03	94.81	69.49	1.11	0.43	0.36
	2	F (8)	1.73	23.18	23.22	0.36	15.77	17.29	0.33	9.21	8.58	0.13	0.03	0.04
			26.27	342.80	280.67	2.36	241.64	219.34	0.86	101.16	61.33	1.50	0.42	0.28
		M (15)	5.04	57.32	48.42	0.40	43.69	39.34	0.28	15.50	10.69	0.26	0.04	0.03
All	All	(41)	24.17	280.85	230.95	2.05	195.47	176.81	0.77	85.39	54.14	1.28	0.44	0.31
			3.78	72.40	61.96	0.45	53.73	48.98	0.37	19.54	14.96	0.29	0.04	0.05

Table 2. Age and sex differences in the energy derived from fat and lean mass metabolism during the moult and mid-year haul-outs and the proportion of lean mass to start lean mass and fat mass as a proportion of end body mass for juvenile southern elephant seals are reported as means with SD below.

Haul-out	Age	Sex	Energy from fat (39.5Mj kg <sup>-1</sup> )	Energy from Protein (17.99Mj kg <sup>-1</sup> )	Daily energy expenditure (Mj d <sup>-1</sup> )	Percentage of energy from fat	Percentage of energy from protein	Fat mass as a proportion of end mass	Proportion of lean mass to start lean mass
Moult	1	F (4)	34.6	4.2	38.8	89.2	10.9	0.2	0.2
			2.8	0.7	3.5	1.0	1.0	0.0	0.0
		M (5)	41.6	3.0	44.6	93.6	6.4	0.2	0.1
	2	F (2)	7.6	1.4	8.6	2.6	2.6	0.0	0.1
			36.2	6.0	42.2	85.8	14.2	0.2	0.3
		M (3)	1.5	0.6	2.1	0.7	0.7	0.0	0.0
Mid-year	1	F (12)	51.0	5.4	56.4	90.4	9.6	0.2	0.2
			7.1	0.8	7.3	1.5	1.5	0.0	0.0
		All (14)	40.8	4.3	45.1	90.5	9.5	0.2	0.2
	2	F (8)	8.2	1.5	8.8	3.2	3.2	0.0	0.1
			43.5	2.8	46.3	93.6	6.4	0.2	0.1
		M (6)	9.8	1.4	9.2	3.5	3.5	0.0	0.0
Mid-year	1	F (12)	51.2	2.8	54.0	94.4	5.6	0.2	0.1
			9.7	2.4	8.4	4.6	4.6	0.0	0.1
		All (15)	43.9	5.0	48.9	89.7	10.3	0.3	0.1
	2	F (8)	5.3	1.6	5.6	3.2	3.2	0.0	0.0
			59.3	4.2	63.5	93.3	6.7	0.2	0.1
		All (41)	10.3	1.4	10.6	2.2	2.2	0.0	0.0
Mid-year	All	(41)	50.5	3.8	54.2	92.8	7.2	0.2	0.1
			11.5	1.8	11.5	3.5	3.5	0.0	0.0

*Table 6.3. The candidate models (GLMs) describing the contribution of terms and their interactions (sample-size-adjusted Akaike Information Criterion weight- AICcwt) to the response variables and significance of terms (analysis of deviance between models) for juvenile southern elephant seals incorporating body mass (m), sex (s), age (a) and haul-out (h). The level of significance shown from the analysis of deviance for significant terms in selected models are shown as  $P < 0.5$  (\*);  $< 0.01$  (\*\*);  $< 0.001$  (\*\*\*)*

Response Variable (Sum of all model weights)	Model terms	AICcwt	Significant terms from analysis of deviance
Mass loss rate (0.68686)	<b>m + h</b>	0.219	mass (***), haul-out (*)
	<b>m + h + m * h</b>	0.113	
	<b>m + a + h</b>	0.073	
	<b>m + h + s</b>	0.073	
	<b>m + a + h + a * h</b>	0.053	
Lean mass loss rate (0.55613)	<b>m + h + s</b>	0.090	mass (***), haul-out (**), sex (*)
	<b>m + a + h + s</b>	0.084	
	<b>a + h + s</b>	0.043	
	<b>a + h</b>	0.039	
	<b>m + h + s + m * h</b>	0.038	
	<b>m + a + h + s + a * s</b>	0.032	
	<b>m + h + s + s * h</b>	0.032	
	<b>m + h + s + m * s</b>	0.032	
	<b>m + a + h + s + m * h</b>	0.029	
	<b>m + a + h + s + a * h</b>	0.029	
	<b>m + a + h + s + m * a</b>	0.028	
	<b>m + a + h</b>	0.027	
	<b>m + a + s</b>	0.091	
Fat mass loss rate (0.54568)	<b>m + a + s + m * s</b>	0.090	mass (***), sex (***)
	<b>m + a + s + a * s</b>	0.063	
	<b>m + h + s + m * s</b>	0.058	
	<b>m + a + h + s + m * s</b>	0.047	
	<b>m + s + m * s</b>	0.045	
	<b>m + a + h + s</b>	0.044	
	<b>m + a + s + m * a + m * s</b>	0.039	
	<b>m + h</b>	0.206	
Start ratio of fat:lean mass (0.69067)	<b>m + h + m * h</b>	0.129	mass (***), haul-out (***)
	<b>m + a + h</b>	0.078	
	<b>m + h + s</b>	0.066	
	<b>m + a + h + m * h</b>	0.052	
	<b>m + h + s + m * s</b>	0.324	
End ratio of fat:lean mass (0.84935)	<b>m + a + h + s + m * s</b>	0.114	haul-out (***), sex (***), mass*sex (*)
	<b>m + h + s + m * h + m * s</b>	0.106	
	<b>m + s + m * s</b>	0.104	
Daily energy expenditure rate (0.73807)	<b>m + a + s + m * s</b>	0.100	mass (***), sex (***)
	<b>m + a + s</b>	0.090	
	<b>m + s</b>	0.066	
	<b>m + a + s + a * s</b>	0.058	
	<b>m + h + s + m * s</b>	0.056	
	<b>m + a + s + m * a + m * s</b>	0.044	
	<b>a + h + s</b>	0.140	
	<b>a + h + s + s * h</b>	0.082	
Percentage of energy from fat (0.55699)	<b>a + h + s + a * s</b>	0.072	mass (*), haul-out (**), sex (***)
	<b>a + h + s + a * s + s * h</b>	0.054	
	<b>m + a + h + s</b>	0.048	
	<b>a + h + s + a * h</b>	0.043	
	<b>m + h + s</b>	0.034	
	<b>m + h + s + m * s + s * h</b>	0.030	
	<b>a + h + s</b>	0.140	
	<b>a + h + s + s * h</b>	0.082	

*Adipose-tissue loss rate*

For the rate of adipose-tissue loss there were significant differences between the sexes and a positive relationship with mass. The candidate models showed strong *mass* and *sex* effects which were both significant in our analysis of deviance (*mass*,  $\chi^2_1 = 27.605$ ;  $P < 0.001$ ; *sex*,  $\chi^2_1 = 15.234$ ;  $P < 0.001$ ; Table 6.3). Keeping all dependent variables constant except *sex*, females used on average 15.7 % less adipose-tissue than males of similar size and age during the same haul-out.

*Ratio of adipose:lean tissue*

At the start of the haul-outs, the ratio of adipose:lean tissue were significantly different between haul-outs and a negatively related to mass. The candidate models showed strong *mass*, and *haul-out* effects, which were both significant in the analysis of deviance (*mass*,  $\chi^2_1 = 15.447$ ;  $P < 0.001$ ; *haul-out*,  $\chi^2_1 = 43.508$ ;  $P < 0.001$ ; Table 6.3). On their return, seals had 18.9 % higher proportions of adipose:lean tissue on average at the start of the mid-year (Fig. 6.4) than at the start of the moult (keeping, *mass*, *age* and *sex* constant). When keeping all dependent variables constant except for mass, an increase in mass decreased the proportion of adipose:lean tissue.

For the ratio of adipose:lean tissue at the end of a haul-out, there were significant differences between sexes and between haul-outs (Fig. 6.4). The candidate models showed strong *haul-out*, *sex* and a *sex\*mass* interaction effects (analysis of deviance: *haul-out*,  $\chi^2_1 = 62.258$ ;  $P < 0.001$ ; *sex*,  $\chi^2_1 = 13.888$ ;  $P < 0.001$ ; *sex\*mass*,  $\chi^2_1 = 5.931$ ;  $P = 0.018$ ; Table 6.3). The *sex\*mass* interaction demonstrated a greater increase in the proportion adipose:lean tissue for females with an increase in mass than for males. Keeping all dependent variables constant except for *sex*, females had on average 13.6 % higher proportions of adipose:lean tissue than males of similar size and age during the same haul-out. In the mid-year the seals had 30.7 % higher proportions of adipose:lean tissue.

*Daily energy expenditure*

The rate of daily energy expenditure showed significant sex and mass differences (analysis of deviance: *mass*,  $\chi^2_1 = 40.474$ ;  $P < 0.001$ ; *sex*,  $\chi^2_1 = 13.647$ ;  $P < 0.001$ ; Table 6.3). On

average, males had a 13.4 % greater daily energy expenditure rate than females and there was a positive increase in daily energy expenditure with as increase in mass (Fig. 6.5).

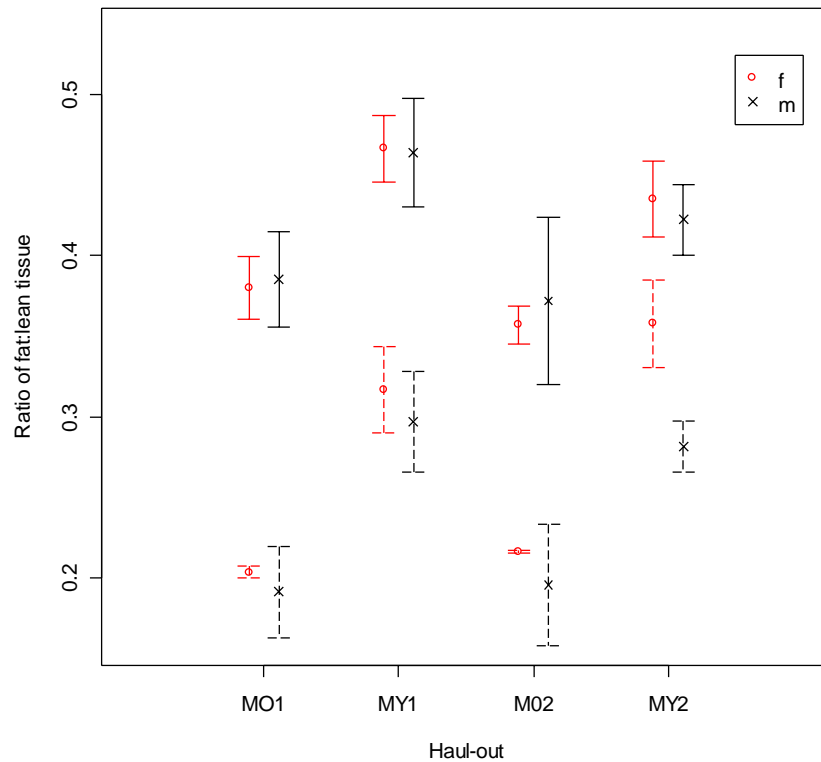


Fig. 6.4. The proportion of fat to lean mass ( $\bar{X} \pm 2SE$ ) at the start (solid lines) and end (dashed lines) of their moult and midyear haul-outs for juvenile southern elephant seals where MO1 and MO2 denote moult and MY1 and MY2 denote midyear haul-outs for one- and two-year-old seal respectively.

#### *Proportion of total energy derived from lipids*

The proportion of energy derived from lipid metabolism was significantly different between sexes and haul-outs. The candidate models showed *mass*, *age*, *haul-out* and *sex* effects, but only *sex* and *haul-out* were significant according to the analysis of deviance (*haul-out*,  $\chi^2_1 = 8.865$ ;  $P = 0.004$ ; *sex*,  $\chi^2_1 = 14.124$ ;  $P < 0.001$ ; Table 6.3). Seals decreased adipose reserves more (3.9 %) during the mid-year than during the moult (Table 6.2). There were also significant differences between the sexes; with males decreasing their adipose reserves more (3.7 %) than females.

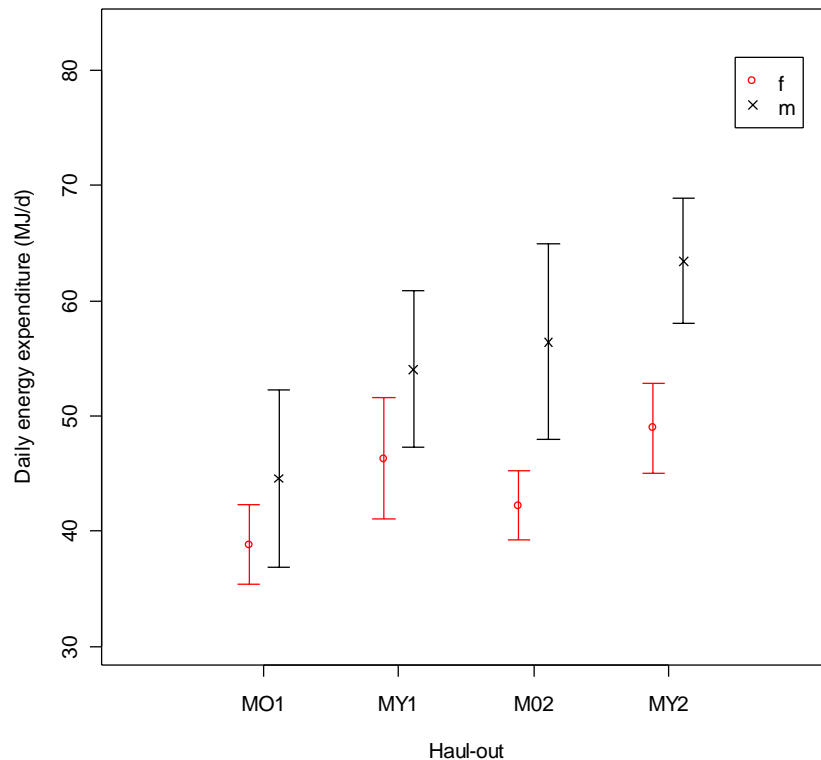


Fig. 6.5. The daily energy expenditure ( $\bar{X} \pm 2SE$ ) for juvenile southern elephant seals, where MO1 and MO2 denote moult and MY1 and MY2 denote midyear haul-outs for one- and two-year-old seal respectively.

#### *End lean mass as a proportion of start lean mass*

The end lean mass as a proportion of start lean mass was important to assess because it addresses whether seals were using more proteinaceous tissue than can be used without over-fasting (defined as using  $> 30\%$  of original lean mass – Castellini and Rea 1992). From our results juveniles used a greater proportion of their lean mass during the moult than during the mid-year haul-out, and moulting females used a greater proportion of their lean tissue than moulting males, but they used similar proportions during the mid-year haul-out (Table 6.2). However, none of the seals used  $> 30\%$  of their original lean tissue mass during either haul-out.

#### *Proportion of adipose mass to the end body mass*

The proportion of adipose mass to the end body mass of the seal is, again, important in understanding if juvenile seals are over-fasting because this will influence the ability to thermoregulate when returning to sea. The seals used a greater proportion of their adipose

in the moult than in the mid-year (Table 6.2), and males used greater proportions than females; however, even in the moult when most adipose tissue was used, no individuals had a body composition of less than 10 % adipose tissue (Castellini and Rea 1992).

## Discussion

Juvenile animals face an uncertain future as they approach maturity, undergoing many morphological, physiological and behavioural changes that influence their energetic requirements and patterns of energy use (Post and Parkinson 2001). As juveniles grow they experience increased absolute energetic demands required for the production of new tissues (Larner 1971; Robbins 1983; Schmitt-Nielsen 1997), and some species such as pinnipeds also need to store some energy for future use (Costa and Williams 1999; Boyd 2002). If these increasing demands are not met this may result in a lower probability of survival or lower lifetime fecundity due to delayed age at first breeding (Brafield and Llewellyn 1982). It is therefore likely that growing mammals will employ a range of energetic strategies in parallel to their changing requirements and environment (Weiser 1994), which could be identified through changes in body composition.

In summary, our data show that 1) in the moult the seals use more energy than in the mid-year which is related to the increased use of lean tissue and to their body composition prior to the haul-out, 2) there are sexual differences in energy use where females used less adipose, but more lean tissue than males. Overall, juvenile mass loss rates during the moult were in the range of those described in other studies of adult elephant seals during their moult (Worthy et al. 1992; Boyd et al. 1994; Hindell et al. 1994b). Although data are available for allometric comparison with adult southern elephant seals and other seal species, I limited our analyses to direct comparisons within the juvenile component of the population.

### *Seasonal differences and haul-out function*

Seasonal differences in juvenile body condition (Lindström 1999; Post and Parkinson 2001) and metabolic rates are common in many species due to both intrinsic and extrinsic factors, but these differences may not affect all age groups identically. Intrinsic differences may be attributed to different cycles of behaviour or hormone regulation such as a breeding, migrating, feeding, moulting or periods of growth (Hedd et al. 1997; Beck et al.

2003a; Rosen and Renouf 1998; Boily 1996; Boily and Lavigne 1997; Norgarden et al. 2003; Nilssen et al. 1997). External influences can include seasonal changes in the environment such as temperature change, changes in the distribution and amounts of food available, or the ability of an animal to find and assimilate those resources (Boily 1996; Anava et al. 2003; Domingo-Roura et al. 2001; Felicetti et al. 2003; Stirrat 2003; Hanel et al. 1996).

A major difference in the behaviour of juvenile and adult southern elephant seals is in their annual haul-out patterns. Only juveniles have a mid-year haul-out, whereas the moult is an essential haul-out for all seals. The timing of the haul-outs and physiological processes of the moult haul-out have been described by many authors (Hindell and Burton, 1988; Worthy et al. 1992; Boyd et al. 1993; Kirkman et al. 2003). During this time seals have an increased energy demand and requirement for protein as has been described for other species (Cherel et al. 1988). As they moult, old skin and hair are sloughed and replaced, a process that requires increased blood supply to the skin and increased energy for thermoregulation and protein for cell replacement. The function of the mid-year haul-out itself remains unclear (Wheatley, 2001; Chapter 4), but without the additional costs of moulting or breeding, it is likely to be relatively inexpensive.

Seals returned to moult with relatively greater amounts of lean tissue than in the mid-year, but they also used more lean tissue during the moult. The metabolism of body reserves is under hormonal control that can mobilize tissues preferentially based on need. As seen in other studies of elephant seals (Noren et al. 2003; Biuw 2003), fatter seals use proportionally more adipose tissue than thinner seals because less lean tissue is available and is not catabolized preferentially. Increased rates of protein catabolism may also be required when replacing their epidermis and growing new hair (Robbins 1993). Therefore, it is still unclear if or how individuals prepare for this additional protein requirement during the previous foraging trip. Individuals may select prey with higher protein content in preparation for this, although it is also possible that this mechanism results from extrinsic factors such as different prey availability throughout the year (e.g., reduced amounts of prey available in winter).

*Sexual development*

Sex differences in body condition and metabolism while ashore have been observed for many species (Field et al. 2001; Winship et al. 2001; Beck et al. 2003a; Aubret et al. 2002; Biuw 2004). Differences within adults have been related to the costs of breeding, especially for capital breeders such as elephant seals (Boyd 2000; Beck et al. 2003a) where energetic costs for females are typically greater. For juveniles, these differences are related to growth rates and precocious development (Schmidt-Neilsen 1997; Siervogel et al. 2003). I found sex differences in the metabolism of lean and adipose tissue in both the moult and mid-year haul-outs, with females tending to metabolize relatively more lean tissue than males. Juvenile males are larger than females (McMahon et al. 1997; Field et al. 2001; Biuw 2004) and grow faster (McLaren 1993); therefore, these differences may be due to females reaching sexual maturity earlier and at a much smaller size than males. This would allow females to preserve more energy in the form of fat to contribute to up-coming breeding effort. This fat-sparing by females supports previous findings by Biuw (2004) where female weanlings had greater fat reserves than males when leaving the beach for their first trip to sea and after subsequent trips. Alternatively, Mellish et al. (2000) suggests that reproductive success of adult grey seals depends more on body protein content than on lipid, though it must be noted that this is for adults that may not be building up lipid stores prior to breeding. McMahon et al. (1997) also showed that most female pups at the time of weaning have all canine teeth whereas all males had not. This supports the observation that females develop earlier and prepare for adulthood in advance of males.

*Are juveniles energetically stressed?*

While the seals are ashore for both the moult and mid-year haul-outs they fast and use energy reserves. When it is time to return to sea they must leave the beach with sufficient amounts of both fat and protein to ensure normal thermoregulation and organ function when they resume travelling and foraging (Cahill, 1979; Cherel et al. 1987; Reilly 1989). In the past it was thought that seals needed to have a lipid content of more than 10 % of total body mass at the end of the haul-out and approximately 70 % of the lean body mass (Castellini and Rea 1992). A recent study by Biuw (2004) has shown that these estimates may be too conservative for juvenile elephant seals embarking on their first trip to sea because many individuals have as little as 50 – 60 % of their original lean mass (total proteinaceous tissue that could be used). Even during the moult when seals have the

greatest protein requirement, they used less than 30 % of initial lean tissue and were therefore able to meet their energetic demands without suffering any consequences of overfasting. Before the moult, seals returned with greater proportions of lean to adipose tissue than during the mid-year, so it remains unclear whether juveniles are preparing physiologically for the moult. After the mid-year haul-out juvenile body composition was around 26 % adipose tissue compared to 20 % during the moult. The reduction in thermal insulation during the moult due to increased peripheral circulation associated with hair growth requires an increased metabolic rate to generate more endogenous heat. These values are higher than the 10 % of body mass suggested by Biuw (2004), so juveniles do not appear to be depleting their fat reserves to critical levels. By adapting the use of fat and protein stores to their seasonal demands and environmental temperature variation, juvenile seals demonstrate a remarkable flexibility to maximize resource accumulation.

Our data demonstrate seasonal differences in the energetic requirements and use of lipid and protein stores of juvenile southern elephant seals. Juvenile elephant seals are expending more energy during the moult, older seals have reduced metabolic rates, and there is differential allocation and use of energy by male and females. We suggest that these differences are most likely related to haul-out function and behaviour, growth and precocious development of females toward sexual maturity though further study is needed on alternative reasons such as changes in hormone balance due to both intrinsic and extrinsic influences. Our refinement of an alternative technique to that of traditional isotopic methods for the measurement of body composition and metabolic rates demonstrates that the modelling of age-specific energy budgets is possible even without detailed physiological data. However, more information on seasonal and intra-specific differences in the diet, foraging behaviour and growth of juvenile seals will assist our understanding of how elephant seals maximize their energy intake and use.

## Summary

Growing juvenile animals undergo many morphological, physiological and behavioural changes that influence their energetic requirements, patterns of energy use and ultimately, their survival and reproductive success. I examined changes in mass loss and body composition of juvenile southern elephant seals, one- and two-year olds, during their two annual haul-outs. At the start and end of the mid-year and moult haul-outs I caught,

weighed and measured 41 and 14 seals, respectively. I measured blubber depth using ultrasound to estimate body composition (lean and adipose tissue mass). Using energy densities of the adipose and lean tissue I calculated total, lean and adipose mass changes and energy expenditure. While moulting, juvenile seals used more energy than during the mid-year, which is related to the increased use of lean tissue for hair and skin regeneration. The amount of energy used increases with mass as individuals mature. I found sexual differences in energy use where females retained greater fat reserves than males, by utilizing more lean tissue. These differences are most likely related to haul-out function and behaviour, growth and earlier development of females toward sexual maturity.



Seasonal patterns of growth in juvenile southern elephant  
seals from Macquarie Island

## Introduction

Quantifying somatic growth and body-mass variation is a fundamental component of understanding the life history of a species (Case 1978; Damuth 1981; Millar 1981; Peters 1983; Wootton 1987; Damuth and McFadden 1990). How rapidly an individual progresses from juvenile to adult status is a trade-off between allocation of resources for somatic growth and development of reproductive potential (Stearns 1992, Roff 1992). In other words, an individual can spend more time growing to a larger size, or it can divert resources to reproduction and sacrifice body size. The resolution of this trade-off is particularly important where food availability and energy use are limit survival and reproductive output (Boyce 1985). Juvenile growth, regarded here as changes in body mass or length with age, can be an important influence affecting survival (Ricklefs 1972; Boyce 1979; Lindström 1999; Coulson et al. 2001; Hall et al. 2001; McMahon et al.2003; Balazs and Chaloupka 2004) and ultimately, rates of population change (Haywood and Perrins 1992; Sand 1996; Boyd 2000; Post and Parkinson 2001; McMahon et al.2003).

Growth can be influenced by both intrinsic (age, sex and developmental physiology) and extrinsic (climate, season and availability of food) factors (Caughley and Sinclair 1994). For example, seasonal growth can affect reproduction and survival for many species (Clutton-Brock et al.1985; Lindström 1999), although previous studies have focused mainly on small predators or long-lived herbivores. Such studies are difficult due to the need for long-term data and the high frequency of captures within annual cycles and across environmental extremes (Caughley and Sinclair 1994). The southern elephant seal, an apex predator in the Southern Ocean (Bradshaw et al. 2003; Hindell et al. 2003), is an excellent model species for studying intrinsic and extrinsic influences that determine juvenile growth strategies in an extremely seasonal environment. Juvenile southern elephant seals have a very distinct annual cycle that is a consequence of living in a seasonal environment, and selective pressure of resource limitation and intra-specific competition (Burton 1985; Chapter 4). They are a highly size-dimorphic, polygynous species, where males at maturity are 8-10 times heavier than females and as such, have vastly different growth rates. Initially, male and female seals grow at similar rates, with females exhibiting a conventional mammalian growth curve with a reduction of growth rate toward puberty (Bell 2004). However, male growth accelerates exponentially after four years of age until reaching maximum body size at approximately 10 years (Bryden 1969; McLaren 1993).

For seals living in a highly seasonal environment, population status and rate of population change can be mediated through food resources (Laws 1956) and that this may be observed in growth-related factors such as changes in age at primiparity, fecundity and survival. The survival of juvenile southern elephant seals (aged 1-4 years) is the most important factor influencing the rate of change of the declining elephant seal populations at Macquarie Island (McMahon et al. 2003). As they progress from juvenile stages toward maturity, an individual's growth rate, and ultimately, its adult body size, may be influenced by ontogenetic changes in morphology and physiology due to sexual divergence and dimorphism, foraging behaviour, the availability of prey, or a combination of these factors (Hindell et al. 1994). Thus, juveniles are hypothesised to be more sensitive than adults to variation in environmental contingencies (Brafield and Llewellyn 1982).

Several functions have been used to describe the growth of pinnipeds (reviewed in McLaren 1993). However, all of these growth functions have in the past been based on relatively small sample sizes and assumed that growth is constant throughout the year. Recent studies of other marine vertebrates have demonstrated a seasonal component to growth and have hence modified traditional growth curves to incorporate this seasonal variation (Eveson et al. 2004; Laslett et al. 2004).

Until now the effects of intrinsic and extrinsic factors on growth, particularly in long-lived species, have been unclear. In this study I describe annual and seasonal growth in length, mass and the associated changes in body composition of southern elephant seals between the ages of one and four years. I test the hypotheses that (i) rates of gain for overall, lean and blubber masses during summer and winter change in relation to seasonal environmental variability of the Southern Ocean and, (ii) that males and females diverge and have different growth strategies in proximate body components due to sexual dimorphism and earlier development toward age at primiparity in females.

## Methods

Four hundred and seventy juvenile southern elephant seals were captured between November 1999 and February 2001 as part of a long-term demographic study of the population on Macquarie Island (Hindell et al. 1994a; McMahon et al. 2003). Data were collected with Australian Antarctic Animal Ethics Committee approval (ASAC 2265 and

1171) and with Tasmanian Parks and Wildlife Service permits. Seals were caught and immobilized as they returned for their moult and mid-year haul-outs (McMahon et al. 2000; Chapter 2). Seals ranged in age from 13- to 46-months at the time of capture and were subsequently allocated into one-, two- and three-year-old age groups. Data collected at the start of the moult haul-out (Nov-Dec) were assumed to reflect austral winter foraging success and associated growth, whereas data from the start of the mid-year haul-out (March-June) are associated with summer foraging and growth.

Seals were caught by hand by placing a canvas bag over the seal's head (McMahon et al. 2000) and physically restrained until anaesthesia was administered intravenously and using prescribed doses (Chapter 2) of a combined 1:1 mixture of tiletamine and zolazepam (Telazol<sup>®</sup>, Forte Dodge, Castle Hill, NSW, Australia). Once anaesthetized, seals were weighed using a digital scale ( $\pm 1$  kg; Dillon ED-2000, Salter Weigh-Tronix Pty Ltd., Victoria, Australia) and a snout-tail length measured (STL;  $\pm 1$  cm; Chapter 2).

*Blubber mass as a percentage of body mass (Body composition)*

For 211 of the captured individuals (45 %), serial lengths, girths and ultrasound measurements of blubber depth were made to calculate body composition (Gales and Burton 1987; Chapter 2). These morphometric measurements were made across seven sections (Fig. 7.1), with the head and hips to the base of the tail forming cones and the rest of the body sections forming truncated cones (Chapter 2). Measures of blubber thickness, corresponding with the girth measurements along the seal's dorsal side were obtained using an ultrasound backfat depth system (A-Scan Plus<sup>™</sup>, Sis-Pro Inc., Woodbury, MN, USA). From these morphometric and ultrasonic measurements, total blubber and lean tissue volumes were calculated and from these I estimated body composition expressed as the percentage of blubber by mass. This method assumed that individuals were circular in cross-section. I also assumed that all the blubber lies in the hypodermis and over the whole body and that the flippers contain insignificant amounts of subcutaneous fat (Chapter 2). Total blubber mass (Slip et al. 1992b; Webb et al. 1998) was calculated by multiplying the blubber volume by the density of blubber, taken as  $0.95 \text{ g cm}^{-3}$  (Gales and Burton 1987). This technique has shown strong agreement with isotopic techniques in the calculation of body composition (Webb et al. 1998) with mean error being  $0.01 \pm 4.25 \%$ . Lean body

mass was calculated by subtracting the blubber mass from the total body mass. Body composition is determined fat mass as a percentage of total body mass.

#### *Modelling rates of mass gain*

To describe the general patterns of overall mass, lean mass and fat mass gain while the seals were at sea, I used the mean arrival body mass and composition values from this study and the mean haul-out duration, mass loss rate and end body composition for each sex and age group during the independent haul-outs (Chapter 5) and unpublished data for three-year-old males and females (Table 7.1).

### Statistical analyses

#### *Seasonal Growth*

Because elephant seals are highly dimorphic, I modelled the growth of males and females separately. I used a maximum likelihood approach, fitting a von Bertalanffy (vB; McLaren 1993) growth function (Equation 1) to individual STL ( $L$ ) and age in days ( $a$ ) of the form:

$$L = L_{\infty} (1 - e^{-k(a-a_0)})$$

where  $k$  and  $a_0$  are constants. Female asymptotic lengths ( $L_{\infty}$ ) were assumed to be 2.57 m (Bell et al. 2005) and 3.11 m for males (Carrick et al. 1962), the approximate length at which the second period of accelerated growth occurs.

I also incorporated a seasonal component to the growth function using an annual periodicity component in combination with the original von Bertalanffy equation. This seasonal component was added by including a sinusoidal function (Eveson et al. 2004):

$$L = L_{\infty} (1 - e^{-k(a-a_0+u \sin(2\pi(a/365-w)))})$$

where  $u$  is the amplitude of the wave and  $w$  is the period. For each analysis I calculated the information-theoretic evidence ratio (ER, an index of the likelihood of one model over another, calculated as the Akaike's Information Criteria (AICc) weight ( $w$ ) of the best model /  $w$  of the next-highest model) (Burnham and Anderson, 2002) as the basis for examining the relative statistical support for which model fitted the data best for each of the sexes.

*Body mass and composition changes*

I compared the body mass ( $n = 470$ ) and composition ( $n = 211$ ) of one-, two- and three-year-old seals between the sexes and the two haul-out periods using general factorial generalized linear models (GLM) in the R package (Ver. 1.9.1, Ihaka and Gentleman 1996). These models also tested for the effect of main factors (e.g., age, sex and haul-out) and all two-way interactions and three-way interactions with mass as the response variable. Examination of the residuals for all models indicated that a Gaussian family error distribution with a log-link were the most appropriate error structures for the input data.

There was no *a priori* reason to assume a single model to describe the contribution of terms and their interactions to the response variables, so I used a form of model selection with sample-size-corrected AICc to select the most-parsimonious model(s) (Lebreton et al. 1992; Burnham and Anderson 2002). To determine the effect of any term seen to be significant in selected models, I used a  $\chi^2$  analysis of deviance. The results of this model selection are shown as the ranked, most-parsimonious models, their individual AICc weight, the significance terms of each model and specific-term tests using analysis of deviance.

## Results

The two-year-old seals were the first age group to return for the annual moult (mean arrival date = 28 Nov) followed by the three-year olds (5 Dec), and finally, the one-year olds (10 Dec). Later in the year, the one-year olds return first for their mid-year haul-out (mean = 22 April), followed by the two-year olds (4 May) and the three-year olds (26 May). The mean body mass and STL of male and female seals ranged from  $167 \pm 22$  kg for one-year olds ( $1.68 \pm 0.09$  m in length) at the start of their annual moult to  $452 \pm 84$  kg ( $2.41 \pm 0.15$  m in length) as three-year olds at the start of their mid-year haul-out. Individuals body size (STL) and mass increased significantly between one to four years of age, and there were some significant differences between seasons and divergence between sexes (Table 7.1).

*Table 7.1. The STL, body mass and condition measured at the start of the moult and mid-year haul-outs for one-, two- and three-year-old southern elephant seals. Also shown are the durations, proportions of mass loss and end body condition, from Chapter 6 and unpublished data denoted by \*, used in the calculation of lean and fat masses at the start and end of a haul-out, and the number of individuals (nbc) used to calculate the body composition at the start of a haul-out.*

Sex	Age	Haul-out	n (nbc)	Age (days)	Haul-out duration (days)*	STL (m)	Body mass (kg)	Body composition (% fat)	Mass loss (%)*	End Body mass (kg)	End Body condition (% fat)*	Lean mass (kg)	End lean mass (kg)	Fat mass (kg)	End fat mass (kg)
Female	1	Moult	47 (13)	418.34 ± 15.04	31.75	1.67 ± 0.09	165.77 ± 24.12	26.15 ± 3.60	31.68	113.25	16.92	122.42	94.09	43.35	19.16
		Mid-year	50 (33)	559.06 ± 55.17	22.75	1.80 ± 0.11	198.50 ± 24.55	30.31 ± 2.59	18.53	161.72	23.97	138.33	122.95	60.17	38.76
	2	Moult	45 (10)	772.24 ± 8.59	32	1.86 ± 0.12	235.29 ± 35.49	27.82 ± 2.26	34.23	154.75	17.70	169.82	127.36	65.47	27.39
		Mid-year	29 (23)	937.69 ± 32.40	22.88	2.03 ± 0.13	290.52 ± 36.38	30.30 ± 1.76	15.71	244.88	26.31	202.48	180.45	88.03	64.43
	3	Moult	50 (10)	1149.86 ± 8.20	38.5	2.18 ± 0.10	345.98 ± 37.59	28.49 ± 2.20	30.46	240.59	19.39	247.39	193.94	98.59	46.65
		Mid-year	4 (3)	1274.50 ± 94.25	21	2.21 ± 0.11	350.75 ± 30.97	29.02 ± 1.61	13.17	304.56	26.52	248.98	223.79	101.77	80.77
Male	1	Moult	38 (9)	432.32 ± 33.25	25.4	1.71 ± 0.08	169.95 ± 19.73	26.94 ± 3.39	24.92	127.60	16.01	124.17	107.17	45.78	20.43
		Mid-year	49 (31)	551.71 ± 51.63	23.5	1.85 ± 0.13	222.14 ± 34.00	29.95 ± 2.69	19.57	178.67	22.82	155.62	137.90	66.52	40.77
	2	Moult	46 (15)	778.65 ± 14.11	33.33	1.95 ± 0.12	246.98 ± 36.78	26.65 ± 1.50	28.52	176.54	16.30	181.16	147.76	65.81	28.78
		Mid-year	33 (25)	928.00 ± 39.68	26.27	2.09 ± 0.14	316.88 ± 53.31	29.11 ± 2.04	18.13	259.43	21.94	224.63	202.51	92.25	56.92
	3	Moult	54 (18)	1144.46 ± 12.83	37.25	2.22 ± 0.12	343.06 ± 45.41	26.15 ± 2.08	26.78	251.19	15.56	253.34	212.10	89.71	39.08
		Mid-year	25 (22)	1311.88 ± 38.77	23.43	2.45 ± 0.13	468.40 ± 77.70	27.13 ± 1.51	17.98	384.18	21.14	341.31	302.97	127.09	81.22

### *Somatic Growth*

Initially, one-year-old males and female seals were similar in STL (males =  $1.71 \pm 0.08$  m, females =  $1.69 \pm 0.09$  m) but diverged in length with age. The sinusoidal vB curve (seasonal vB) allowing for seasonal differences fitted our data better than a general vB curve (Fig. 7.1), using the AICc weight evidence ratio the seasonal vB growth model significantly improved the fit for males and females (by 198 times for males and 1.92 times and females), and reduced the residual standard errors (Table 7.2). This seasonally adjusted vB growth curve shows that males grew rapidly after their annual moult (austral summer), but had reduced growth after their mid-year haul-out through the winter. Although still had a seasonal component to growth, this was less pronounced than for males and they grew more continuously throughout the year.

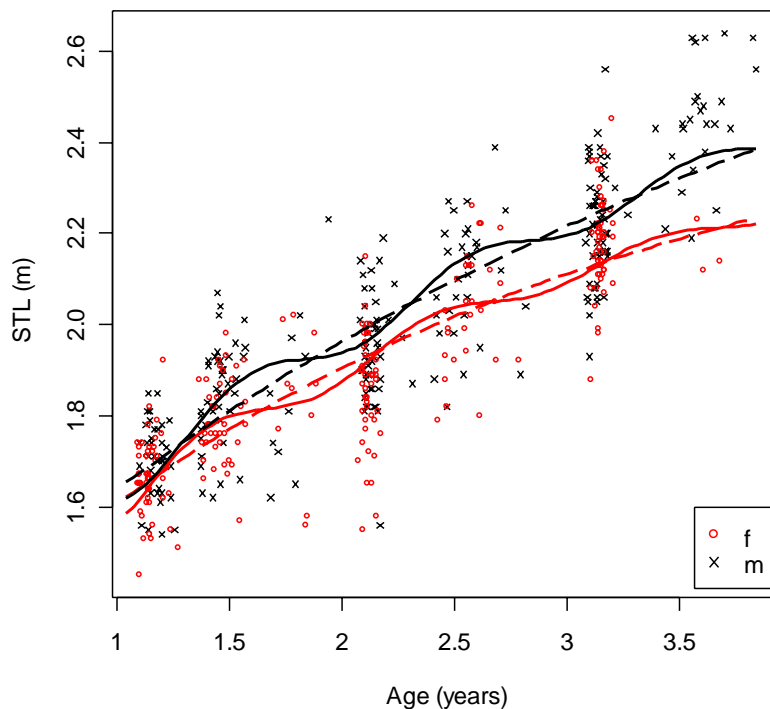


Fig. 7.1. von Bertalanffy (vB) and seasonal vB growth curves for one-, two- and three-year-old southern elephant seals are shown as dashed and solid lines, respectively (black = males; red = females).

### *Age and sex differences in size*

As with STL, there were significant age, sex and seasonal differences in body mass (Table 7.1; Fig. 7.2). The best two candidate models showed strong *age*, *sex*, *haul-out* effects and a *sex\*haul-out* interaction (analysis of deviance: *age*,  $\chi^2_1 = 1756.6$ ;  $P < 0.001$ ; *sex*,  $\chi^2_1 =$

17.98;  $P < 0.001$ ; *haul-out*,  $\chi^2_1 = 40.31$ ;  $P < 0.001$ ; *sex\*haul-out*,  $\chi^2_1 = 12.417$ ;  $P < 0.001$ ; Table 7.3). Therefore, there were significant overall increases in mass with age, males were larger than females and seals were larger in the mid-year than in the moult. More importantly, there was also a significant *sex\*haul-out* interaction due to male and female masses being similar during the mid-year haul-out for a given age, but different in the moult. Similar to somatic growth, males increased in mass more rapidly than females in the summer, but then did not increase in mass at a similar rate during the winter. Females continued to gain mass more consistently throughout the year.

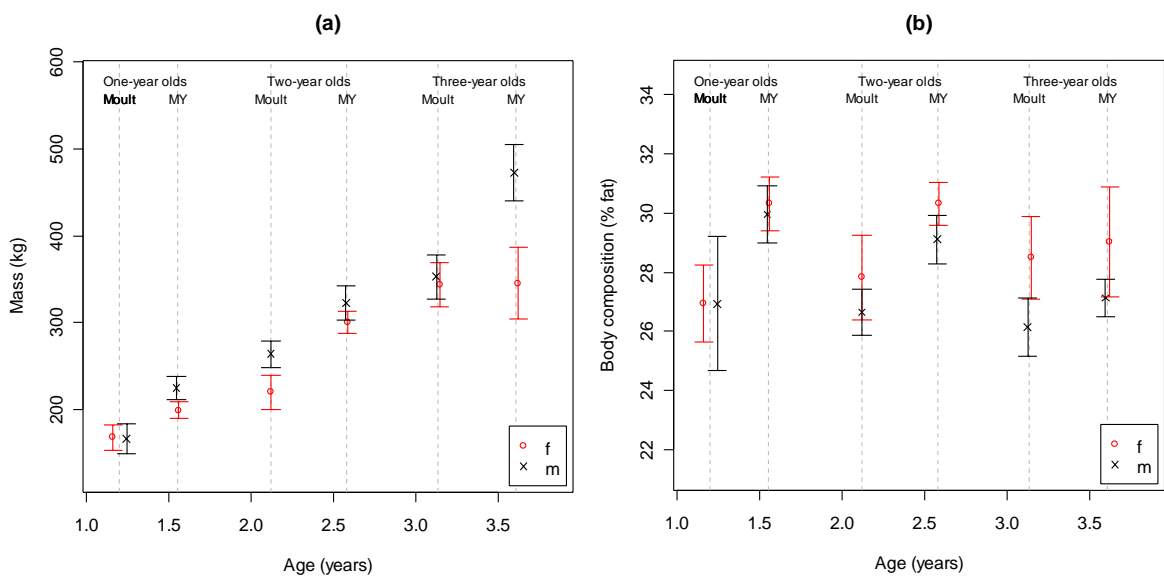


Fig. 7.2. a) Body mass and b) body composition (% fat) at the start of the moult and midyear haul-outs for one-, two- and three-year-old southern elephant seals.

Table 7.2. General and seasonal von Bertalanffy growth model parameters for juvenile southern elephant seals from Macquarie Island.

Sex	Growth function	n	k	a0	u (seasonal VB only)	w (seasonal VB only)	Residual standard error	df
Females	vB	225	0.00079	758.8			0.1149	223
	Seasonal vB		0.00079	741.8	46.28	0.18	0.1139	221
Males	vB	245	0.00068	728.8			0.1256	243
	Seasonal vB		0.00068	752.5	-49.92	0.17	0.1225	241

*Table 7.3. The candidate models (GLMs) describing the contribution of age (a), sex (s) and haul-out (h) and their interactions (sample-size-adjusted Akaike Information Criterion weight- AICcwt) to body mass and composition and significance of terms (analysis of deviance between models) for juvenile southern elephant seals. The level of significance of GLM terms, in bold, and from the analysis of deviance for significant terms in selected models are shown as  $P < 0.5$  (\*);  $< 0.01$  (\*\*);  $< 0.001$  (\*\*\*)*.

Response Variable (Sum of all model weights)	Model terms	AICcwt	Significant terms from analysis of deviance
Mass (0.68028)	<b>a + s + h + s*h</b>	0.42963	age (***), haul-out (**), sex (***),
	<b>a + s + h + s*h + a*h</b>	0.25064	sex*haul-out (***)
Body Composition (0.58513)	<b>a + s + h + s*h + a*h</b>	0.58513	age (***), haul-out (**), sex (***), age*haul-out (***), sex*haul-out (***)

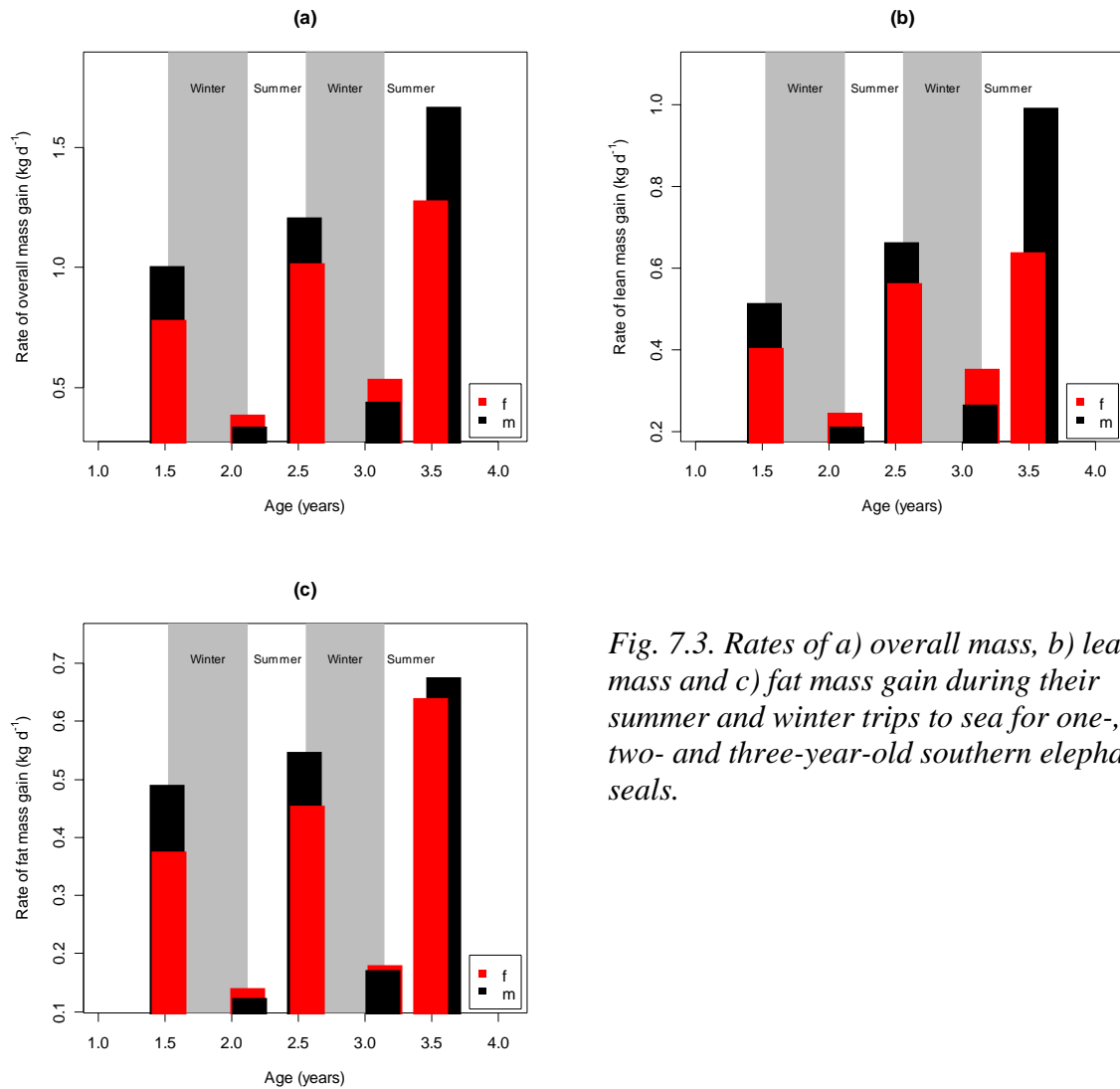
There were also significant age, sex and haul-out differences in body composition (BC). One candidate model was chosen as the most parsimonious model showing strong *age*, *sex*, *haul-out* effects and support for an *age*\**sex* and an *age*\**haul-out* interaction (analysis of deviance: *age*,  $\chi^2_1 = 11.67$ ;  $P < 0.001$ ; *sex*,  $\chi^2_1 = 12.27$ ;  $P < 0.001$ ; *haul-out*,  $\chi^2_1 = 58.08$ ;  $P < 0.001$ ; *age*\**sex*,  $\chi^2_1 = 9.66$ ;  $P = 0.002$ ; *age*\**haul-out*,  $\chi^2_1 = 13.68$ ;  $P < 0.001$ ; Table 7.3). As the one-year-old seals return for their moult and mid-year haul-outs, their BCs were significantly different, although male and female BCs were similar at these times. However, as individuals age, male and female BCs become significantly different with females having greater proportions of fat than males.

#### *Modelled rates of mass gain*

To describe rates of body mass, lean mass and fat mass gain (Table 7.4; Fig. 7.3) for an average seal during the winter and summer, I used the overall mean body masses and BCs of the different age seals at the start of the moult and mid-year haul-outs, and mean haul-out durations, proportion of mass loss and BCs at the end of the respective haul-outs (Table 7.1). These modelled data clearly show that during summer, the rate of body, lean and fat mass gain are almost double that observed during winter. Overall mass gain shows a similar pattern, with somatic growth showing an increased gain in summer and divergence between males and females. However, changes in mass gain for lean and fat tissue may be more interesting. For lean mass gain, males have increased gain in summer but lower lean mass gain in winter than females. For fat mass there is again a similar pattern; males gain more fat mass in summer, though in winter their fat mass gain appears similar.

*Table 7.4. Overall mass, lean mass and fat mass gains over their summer and winter trips to sea for one-, two- and three-year-old southern elephant seals*

Sex	Age	Season	Time at sea (days)	Overall mass gain (kg)	Lean mass gain (kg)	Fat mass gain (kg)	mass gain (kg d <sup>-1</sup> )	Lean mass gain (kg d <sup>-1</sup> )	Fat mass gain (kg d <sup>-1</sup> )
Female	1	Summer	108.97	85.25	44.24	41.00	0.78	0.41	0.38
		Winter	190.43	73.57	46.87	26.70	0.39	0.25	0.14
	2	Summer	133.45	135.77	75.12	60.64	1.02	0.56	0.45
		Winter	189.29	101.10	66.94	34.16	0.53	0.35	0.18
Male	3	Summer	86.14	110.16	55.03	55.12	1.28	0.64	0.64
		Winter	203.44	68.31	43.27	25.04	0.34	0.21	0.12
	1	Summer	94.00	94.55	48.45	46.10	1.01	0.52	0.49
		Winter	116.02	140.34	76.87	63.47	1.21	0.66	0.55
	2	Summer	190.19	83.63	50.83	32.80	0.44	0.27	0.17
		Winter	130.17	217.21	129.21	88.00	1.67	0.99	0.68



*Fig. 7.3. Rates of a) overall mass, b) lean mass and c) fat mass gain during their summer and winter trips to sea for one-, two- and three-year-old southern elephant seals.*

## Discussion

Growth is an energetic trade-off with future fecundity, contemporary maintenance and increasing body size. Thus, patterns in growth rates can influence reproductive success and survival (Post and Parkinson 2001); however, they may show seasonal plasticity to remain “optimal” (Abrams et al. 1996). Although seasonal differences in growth have been found for many species (Stearns 1992; Roff 1992), they are often related to reproductive or physiological state (intrinsic factors) or to environmental influences (extrinsic factors). However there have been few studies on these factors influencing intermediate growth, once energy stores provided by maternal investment have been depleted, that would have great effects on an individual’s survival and population demography (Lindström 1999). Southern elephant seals are long-lived predators that are active throughout the year in an

extremely seasonal environment. Therefore, both extrinsic and intrinsic factors influence juvenile growth strategies, immediate survival prospects and subsequent breeding success. Our analyses revealed clear patterns in somatic growth (in terms of body length), changes in mass (overall, lean and blubber masses) and body condition that may highlight the interactions of sexual development and food availability/quality influences on growth over time resulting in different growth strategies toward maturity. There was a pattern of greater somatic growth during summer than in winter, which is most likely related to extrinsic factors such as energy acquisition, the availability and quality of food or environmental influences that may exclude smaller animals from resources such as lower temperatures or physical barriers (Sand 1996). However, there were also important differences between male and female growth patterns, which are likely to be due to intrinsic factors. Males were larger, leaner and grew faster than females due to differential energy allocation to the relatively earlier sexual development of females (Bryden 1969; McMahon et al. 2003; Biuw 2003; Chapter 5).

#### *Extrinsic influences and energy acquisition*

Seasonality in environmental conditions is a major influence on growth for many species (Clutton-Brock and Albon 1989; Stearns 1992; Roff 1992, Lindström 1999) through climatic changes and the energetic cost of thermoregulation (Sand 1996), and changing availability or quality of food (Dietz et al. 1994; McCafferty et al. 1998). Primary productivity in the Southern Ocean is highly seasonal due to strong fluctuations in light intensity and ice cover (Arrigo et al. 1998). Juvenile southern elephant seals from Macquarie Island spend around 90 % of their time south of the Polar Front in summer and the majority (around 75 %) of their time farther north, between the Polar Front and the southern boundary of the Antarctic Circumpolar Current during winter (Field et al. 2004a). Although little is known about the distribution of elephant seal prey in the Southern Ocean (Rodhouse and White 1995) especially during winter, our study demonstrated that juvenile seals grow almost twice as fast in summer than in winter. Furthermore, the amount of time at sea for an average seal during winter is almost double the summer trip duration (Chapter 4), even though absolute mass gain is greater in summer. Therefore, it is likely that there may be a decrease in both the availability and/or quality of prey available to juvenile seals in winter. This may be compounded by the exclusion of younger smaller seals from remaining farther south due to the presence of ice.

*Intrinsic influences and energy allocation*

For many species, seasonality in growth has been attributed to sex, age and physiological or reproductive states (Clutton-Brock et al. 1985; Clutton-Brock and Albon 1988; Loudon 1989; Caughley and Sinclair 1994; Warrick and Cypher 1999; Winstanley 2000; Peltier and Barboza 2003; Beck et al. 2003a; Vieberg et al. 2004). All juvenile mammals need to grow to reach maturity, but the rate at which they do so may influence their age at primiparity, lifetime fecundity or the probability of survival (Post and Parkinson 2001). For growing juvenile southern elephant seals, there are two main intrinsic influences on growth: their allocation of energy for their annual moult and, though not directly related to breeding, their allocation of energy to rapid growth of males due this species' sexual dimorphism.

As such, juveniles need to balance the energy allocated to growth against storage during periods of resource scarcity or additional metabolic costs (e.g. moulting). Juvenile southern elephant seal fare well in summer with both increased growth rates and increased energy reserves. Although the true function of the mid-year haul-out is debatable, it may serve to reduce intra-specific competition for food resources (Chapter 4). In contrast to their summer foraging and mid-year haul-out, seals return after the winter foraging trip with a greater proportion of lean tissue to blubber and a reduced overall mass gain. Although this may be in part due to reduced availability of food, it may also be influenced by the different energetic requirements for moulting. Because seals allocate more energy to the provisioning of lean tissue in preparation for the moult, it is likely they possess the additional energy required for increased somatic growth.

Body size has been shown to increase reproductive success in highly dimorphic species (Roff 1992; Stearns 1992), and rapid growth is important for reaching the body size and condition required for breeding (Brown et al. 1993, Clinton and Le Boeuf 1993). For a number of pinniped species, early growth and survival is influenced by maternal energy expenditure (Baker and Fowler 1992; McMahon et al. 2003) though this has been questioned for male northern elephant seals (Clinton 1994). The general growth pattern of the seals in this study are similar to that seen for other southern elephant seal populations though are different to those presented by Clinton (1994) in which males grow almost

continuously after approximately one year old without a second growth spurt around puberty.

After accounting for variation in parental expenditure, a juvenile's growth rate may be the most important determinant of breeding success and survival (Lindström 1999). A recent review of sexual segregation (Ruckstuhl and Neuhaus 2000) highlighted the potential of differential activity budgets in the life history of mammals which would also influence growth, where males take more risks when foraging in order to increase growth whereas females select less risky foraging environments to minimize potential variation in diet and predation that will have consequences for their offspring. Therefore, I suggest that southern elephant seals possess different growth strategies in relation to their activity budgets. Initially, one-year-old male and female body masses and energy reserves are similar. During the austral summer, all juveniles increase in length and body mass, but also increase their blubber stores. During winter, however, two different growth strategies related to energy allocation become evident. Juvenile females continue to grow in length and mass while storing energy mostly as blubber. Males grow more slowly, but they become longer and leaner by allocating relatively more energy lean tissue. Also, an increase in body size has been shown to increase dive duration (Hindell et al. 1999) and depth and when combined with the spatial segregation at-sea would further reduce intra-specific competition (Chapter 4). These physiological strategies enable males to increase body size (measured as length and mass) more quickly than females, while females prepare for earlier maturity and the onset of breeding and may serve to reduce further intra-specific competition between sexes and age groups.

#### *Seasonal growth and survival*

The evolution of different growth strategies appears to provide the sexes with the means to maximise their long-term reproductive success when exploiting food resources in an extremely variable and seasonal environment. The female strategy of moderate growth to reproductive size and condition maximises the probability of reaching breeding age (Festa-Bianchet et al. 2000) where energy stores may be required when food is limited. However, males increase the relative allocation of energy to somatic growth to attain a mating advantage despite having a decreased probability of survival during times of reduced resource availability. A divergence in survival for male and female seals has been observed

(McMahon et al. 2003) with males having lower survival than females for which our data may now provide a proximate cause.

Juveniles are potentially the most sensitive component of population demography to variation in environmental factors affecting resource availability (Lindström 1999). Evidence from this study, combined with their at-sea spatial use (Chapter 4) show differential growth and habitat use which would both reduce competition for resources and promote optimal resource allocation for growth (body size and condition) and maintenance increasing an individual's probability of survival and future breeding success. Therefore, I hypothesise that a decrease in food availability reduces the energy available for growth, resulting in (1) a reduction in winter survival for males and (2) a delay in the age at primiparity for females. Thus, long-term changes in food availability, especially in winter, linked with differential development between sexes are likely to affect entire cohorts and have a strong influence on rates of population change. Differences in growth rates with northern elephant seals may reflect different food availability or foraging behaviour and should be investigated further to understand the influence of environmental variation on evolutionary growth strategies.

### Summary

Conditions experienced in early life affect growth and influence life-history strategies. Although seasonality in growth has been studied for many species, its influence on the growth strategies of long-lived predators is poorly understood. The Southern Ocean is an extremely seasonal environment in which southern elephant seals spend the majority of their annual cycle. We examined the variation in length (somatic growth), body mass and composition (condition) of juvenile elephant seals ( $n=470$ ) between the ages of one and four years in relation to different growth strategies. Overall, there was a pattern of greater somatic growth rate in summer than winter, which is most likely related to seasonal variation in the quality and quantity of prey available. Males were larger, leaner and grew faster than females, demonstrating the strategies to attain maximum size quickly in males, and to breed earlier in females. We suggest that differential growth strategies, linked with changes in habitat use, reduce competition for resources and promote optimal resource allocation for growth in juveniles, thus increasing an individual's probability of survival and future breeding success.

## Thesis Conclusions

Southern elephant seals show the highest degree of sexual dimorphism in size amongst all mammal species. They have a circumpolar distribution around Antarctica and the sub-Antarctic islands of the Southern Ocean, an environment which shows great seasonal variation in climate and productivity. Elephant seals are as equally adapted to living on land and as in water. They are exceptional mammals, capable of diving to depths greater than 1000 m and remaining submerged for over an hour during their first trip to sea after weaning (M. Biuw, unpublished data). These diving abilities increase with age (Le Boeuf et al. 1996; Hindell et al. 1999; Irvine et al. 2000; Le Boeuf et al. 2000), and adults can dive to depths more than 1500m and for longer than 100 min. Like many large mammals they are long-lived, grow relatively slowly (over many years and seasons), have delayed maturation and invest heavily in the few offspring born each cycle (Boness et al. 2002). As such, if any species is able to show its evolutionary adaptations over the course of a multi-year study to constraints imposed by the rigours of their environment, it is the southern elephant seal.

The aim of this study was to examine the ecological factors and their evolutionary implications that have shaped the behaviour and physiology of juvenile southern elephant seals dictating the path to sexual maturity. During this stage, individuals undergo many morphometric and physiological changes which incur additional energetic costs to those required for maintenance, and these must be met for an individual to survive and fulfil its potential fecundity (Sibly and Calow 1983). Once the energy stores acquired from maternal provisioning are gone, an individual's probability of survival will depend on its ability cope with unpredictable environmental variation. As such, the juvenile stage involves a constant trade-off between energy allocation (maintenance, growth and development) and energy acquisition (foraging ecology); both are affected by biological (intrinsic) and environmental (extrinsic) stochasticity. Therefore, it is likely that fluctuation in the availability of food resources will affect this demographic group, and thus rates of population change more than others (McMahon et al. 2003).

Juvenile southern elephant seals live and forage in a highly seasonal environment. Due to their life cycle, energy acquired during two or three extended periods at sea each year is allocated to (i) maintenance, (ii) growth and (iii) storage for functional haul-outs, which are periods of elevated energetic usage for moulting (or breeding as adults). By monitoring

individual seals over their life cycle we have been able to observe changes in foraging behaviour, diet, mass and body composition that demonstrate the relative success of different foraging periods and the subsequent use of the accumulated energy stores. If we assume that elephant seals are trying to maximise their net energy gain to reach maturity as soon as possible, describing the foraging ecology, growth and development patterns of this demographic group will elucidate the important proximate processes affecting population dynamics.

This study has demonstrated a number of sex and environment related interactions in growth and development as the seals mature. Although in each chapter I described the patterns within an ecological and evolutionary context, this chapter will synthesise these to describe the ontogenetic processes influencing the evolutionary processes of elephant seal populations.

The most important determinants of juvenile survival of any species are probably foraging success and predation (McNamara and Houston 1987) though the importance of disease has been increasing apparent in recent years (Harwood and Hall 1990; Hall et al. 2001; Linn et al. 2001). Southern elephant seals have few known predators (Condy et al. 1978; Guinet et al. 1992; McMahon 2003), and thus it is more likely that the availability and quality of food resources are the most important components influencing energy acquisition and survival (Sæther 1997).

### Influences on energy acquisition

Juvenile southern elephant seals have exhibited seasonal differences in habitat use. Seasonality, in both climate and the availability and quality of resources (habitat and food) has been shown to influence the foraging ecology of many species (e.g. Sand 1996; Domingo-Roura et al. 2001; Felicetti et al. 2003; Peltier and Barboza 2003). Summer and winter in the Southern Ocean are distinguished by large differences in light intensity and ice cover (Arrigo et al. 1998), with decreased productivity due to the expansion of ice cover and decreased light levels during winter. These seasonal changes may limit juvenile seals in their potential habitat due to their reduced capacity to deal with heat loss relative to adults (Thompson et al. 1998).

After environmental factors affecting the availability of resources, foraging success is influenced primarily by inter- and intra-specific competition. These two sources of competition have been identified as a significant component in the evolution of niche width (Polis 1984; Schoener 1986; Bolnick et al. 2003). Ontogenetic niche shifts (Woodward and Hildrew 2002) have been proposed for many species as the major component of total niche width attributed to age/size structure (Warren 1996; Williams and Martinez 2000; Bolnick et al. 2003) and act to partition resources and maximize an individual's foraging success, especially when resources are limited and environmental predictability is low (Adams 1996; Perry 1996; Hamilton and Barclay 1998; Kato et al. 2000; Wikelski and Wrege 2000; Bowen et al. 2002; Pearson et al. 2002; Bradshaw et al. 2003; Beck et al. 2003b; Radloff and Du Toit 2004). Therefore, ontogenetic changes in morphology, habitat use and foraging behavior may promote population stability more effectively over evolutionary time than competing for resources when they are limited (Polis 1984). These are density-dependant effects and as the Macquarie Island population has been declining for almost half a century (McMahon et al. 2003) it is unlikely that the population is near carrying capacity. Although it is unlikely that effects are acting as selective forces today, they are likely to reflect recent evolutionary strategies (i.e., from 150 years ago when the population was at carrying capacity). Alternatively, as the populations of elephant seals are stabilizing in the Indian sector of the Southern Ocean, a new equilibrium may have been found between population size and resources and ontogenetic changes may once again be advantageous (Hindell 1991).

As juvenile southern elephant seals age and grow, they use a greater area of the Southern Ocean (Chapter 2&3) and their diving ability, with respect to duration and to a lesser extent depth, increases (Le Boeuf 1996; Hindell et al. 1999; Irvine et al. 2000) and these are reflected by changes in diet composition and prey size (Chapter 4). Although their diving behaviour is a complex interaction between physiological, morphological and behavioural changes associated with age and size, in general seals are able to dive deeper and remain at depth for longer as they age. These changes in patterns of spatial use, diving ability and diet, potentially reduce intra-specific competition for resources and allow the different age groups to become separate 'ecological species', thus maximising their potential foraging success.

### Energy allocation strategies

In recent years the development of evolutionarily stable strategy (ESS) theory has provided an analytical framework to examine the decisions of individuals toward maximum fitness in relation to the decisions of others (Parker and Maynard Smith 1990). This is important in a stochastic environment where foraging success may already be density dependent.

Juvenile growth has been defined as a trade-off in energy allocation with future reproductive potential, maintenance and storage for use during times of food scarcity (Post and Parkinson 2001). This interaction for resource allocation is important as it affects both an individual's survival and reproductive potential (Hirshfield and Tinlake 1975). Although an individual's growth rate is not considered in most life history models, it does determine the age of primiparity (Sand 1996) and juvenile survival which are the primary determinates of lifetime reproductive success (Post and Parkinson 2001). For many species of long-lived vertebrate, increased adult body size confers reproductive advantages (for example Le Boeuf and Reiter 1988; Sydeman and Nur 1994) and as such, maximising growth is important for reaching adult size and lifetime reproductive success. An individual that grows rapidly, reaches age and size of first breeding sooner and maximise the number of potential offspring. However, this rapid growth comes at a cost of reducing the probability of survival (Sadler 1969; Boyce 1985, Stearns 1992). An alternate strategy is to grow more slowly and retain some energy in reserve against resource scarcity. In highly variable environment with seasonal and inter-annual changes in food availability an individual's own survival is more important and will ultimately increase lifetime reproductive success (Sæther 1997; Lindström 1999).

Overall, juvenile males are larger, leaner and grow faster than females. This is an interesting pattern because it appears that males are allocating greater energy to somatic growth even when food is seasonally limited. Differences between sexes in growth and development strategies may enable males to increase body size more quickly than females, which may be crucial if males are to grow to such large adult male size (~ 4000 kg) and maximise their potential fecundity. In accordance with life history theory (Clutton-Brock et al. 1985) males increasing their relative allocation of energy to somatic growth to attain a mating advantage may also decrease their probability of survival during times of reduced resource availability, though this has been questioned for northern elephant seal males (Clinton 1994). Alternatively, females prepare for earlier maturity and the onset of

breeding (Sydeman and Nur 1994; Boyd 2000) to increase their lifetime fecundity. The female strategy of moderate growth to reproductive size and condition maximises the probability of reaching breeding age (Festa-Bianchet et al. 2000) where energy stores may be required when food is limited.

### Overall Summary

Theory predicts that the evolution of life history will contain physiological trade-offs that relate to the 'optimal' allocation and use of energy throughout an individual's life to maximise lifetime reproductive output (Parker and Maynard Smith 1990; Stearns 1992; Roff 1992; Charnov 1997). This study has focused on the acquisition and allocation of energy as it changes through the most energetically flexible stage of an individual's life to determine how and why observed patterns may influence an individual's probability of survival. One direction of future study may be the analysis of summer and winter effects on survival for the juvenile age groups to see if winter is a period of lower survival and how this subsequently influences population dynamics.

Juvenile southern elephant seals have patterns of differential sexual development and divergence in growth that are superimposed on intra-annual environmental variation in habitat and availability of food. Ontogenetic differences in timing of haul-outs, habitat use and diet may act to reduce competition for resources through niche expansion. This allows optimal resource allocation for growth (body size and condition) necessary in a highly dimorphic, polygamous species. However, in an environment where resources are limited seasonally and subject to stochastic variation, different growth strategies will evolve to maximise reproductive fitness.

The evolution of different growth strategies appears to provide the sexes with the means to maximise their long-term reproductive success. Indeed, my results appear to provide a proximate cause for the observed lower probability of survival in male juveniles as suggested by McMahon et al. (2003) and a changing age of primiparity through seasonal variation in food availability. Thus, long-term changes in food availability, especially in winter, linked with differential developmental between sexes are likely to affect entire cohorts and strongly influence rates of population change.

Southern and northern elephant seals have similar morphology and physiology. However for such similar species this study has demonstrated that they have evolved very different growth strategies, particularly between males. These differences have provided us with an excellent opportunity for future research using comparative life history studies to examine the effects for environmental variation on the evolution of these growth strategies.



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