

**FORAGING ECOLOGY OF  
SOUTHERN ELEPHANT SEALS  
FROM HEARD ISLAND**

by

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A thesis submitted in fulfilment of the requirements  
for the degree of

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### **Declaration**

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



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A handwritten signature in blue ink, appearing to read 'Slip', is centered on the page.

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For when the *matkas* seek the shore to drop their pups aland,  
The great man-seal haul out of the sea, aroaring, band by band;  
And when the first September gales have slaked their rutting-wrath,  
The great man-seal haul back to the sea and no man knows their path

- *Rudyard Kipling, The Rhyme of the Three Sealers*

Frontispiece (previous page): Adult male southern  
elephant seal at Heard Island, September 1992.

## ABSTRACT

1. The foraging ecology of the southern elephant seal population at Heard Island was examined. The study aimed to quantify the current status, diet, movement patterns, and foraging behaviour of the population in order to use this information to make an estimate of the population's energy requirements and food consumption.
2. I compared intravenous and intramuscular administrations of ketamine and diazepam to immobilise juvenile (8 to 24 months old) southern elephant seals (*Mirounga leonina*), to determine the most appropriate method for immobilising seals to a level required for stomach flushing or attaching electronic activity recorders. With intravenous injections, time to induction was shorter and less variable, the duration of immobilisation was shorter and less variable, and dose of ketamine was lower and less variable. Eight of 32 seals (25%) injected intravenously had apnoeas ranging from 8 to 20 minutes (mean =  $16 \pm 4.5$  min), and 6 of 27 seals (22%) injected intramuscularly were apnoeic for more than 5 minutes. Seals which became apnoeic after intravenous injection began breathing before the theoretical aerobic dive limit was reached.
3. I surveyed the southern elephant seal population at Heard Island regularly from February 1992 until March 1993, and the haulout patterns of the major components of the population were determined. During the breeding season 14277 adult females were counted. Raw counts were corrected using two models, one purely mathematical and the other based on the haulout behaviour of female seals. Total pup production was estimated at between 17000 and 18000 for 1992. Previous counts of elephant seals from 1949-51, 1985 and 1987 were corrected using the same models. The population declined by about 50% between 1949 and 1985 but there appears to have been little change from 1985 to 1992.
4. Stomach contents were lavaged from 76 southern elephant seals at Heard Island between July 1992 and March 1993. Eighty-six percent of stomachs contained cephalopods from

17 species. Numerically the most important was *Psychroteuthis glacialis* (21.1%), and from estimated biomass the most important was *Kondakovia longimana* (40.4%). Three other species were also common prey: *Moroteuthis knipovitchi* (19.4% by estimated biomass), *Moroteuthis ingens* (13.0%), and *Alluroteuthis antarcticus* (10.2%). Sixty-six percent of stomachs contained fish remains, and four species, *Dissostichus eleginoides*, *Electrona carlsbergi*, *E. antarctica*, and *Gymnoscopelus nicholsi*, were identified from otoliths. The diet of adults differed from that of juveniles, particularly pups in their first year. *Martialia hyadesi* was the most important prey of juveniles and represented 57.1% of estimated biomass consumed. Furthermore, smaller seals ate smaller squid. The species and size of cephalopods eaten by southern elephant seals are similar to those of other Southern Ocean predators, particularly species of beaked whales.

5. I investigated the foraging ranges and diving behaviour of adult southern elephant seals from Heard Island using archival geolocating time depth recorders. Most seals moved south to Antarctic waters, migrating long distances to foraging grounds that are related to oceanographic features, such as the Antarctic continental shelf and the Kerguelen Plateau. During the post moult migration adult females moved an average of  $2502 \pm 939$  km, and adult males moved an average of  $1749 \pm 929$  km away from Heard Island. Post moult adult males moved further south than adult females and foraged mainly over the continental shelf, while females foraged mainly in pelagic waters of the pack ice zone and only occasionally moved over the shelf area. During the post breeding migration adult females moved an average of  $1186 \pm 673$  km away from Heard Island and concentrated their activity at the edge of the Kerguelen Plateau. Seals travelled faster in the first week away from Heard Island than at other times. Diving activity was concentrated between 200 and 800 m depth, and was occasionally related to thermal discontinuities in the water column but at other times was not.
6. Diving behaviour of two juvenile southern elephant seals from Heard Island, 9 to 11 months of age, during their second trip to sea was examined using time depth recorders.

Dive behaviour was recorded for 76 days for the juvenile male and 66 days for the juvenile female with 6652 and 4566 dives recorded respectively, which represented about 65% of the trip to sea. Mean dive duration was  $15.5 \pm 5.1$  minutes with a maximum of 39 minutes for the juvenile male (departure mass 168 kg, return mass 192 kg), and mean dive depth was  $323 \pm 157$  m with a maximum of 834 m, while for the juvenile female (departure mass 163 kg, return mass 188 kg), mean dive duration was  $21.1 \pm 6.4$  min with a maximum of 58 min, and mean dive depth was  $416 \pm 147$  m with a maximum of 1270 m. Diving was continuous and over 90% of the time at sea was spent underwater, with only brief periods at the surface. Mean surface intervals were  $1.67 \pm 2.54$  and  $1.63 \pm 0.94$  min, for the male and female respectively, and extended surface intervals greater than three minutes represented less than 2% of all surface intervals for either seal. Both animals remained at sea for the entire period of August to November and showed patterns of continuous, deep, long duration diving with short surface intervals. Dive profiles consistent with pelagic foraging were common. Locations determined from sea temperature profiles suggest that these animals were foraging in mesopelagic waters in mid ocean, both north and south of the Antarctic Polar Front, and at times over the edge of the Kerguelen Plateau.

7. A model of energetic costs of reproduction, foraging, growth, moult and haulout was used to calculate energy expenditure for different age classes of southern elephant seals that breed at Heard Island. This was combined with data on age structure and population size to estimate the energetic requirements of the population. Estimates of energy consumption were converted to food consumption based on current knowledge of the diet of the Heard Island population. Data on the foraging behaviour and movements of elephant seals from Heard Island were used to estimate the amount of food consumed from the Kerguelen Plateau. Energy expenditure associated with foraging contributed 56.2% and 65.3% of total annual energy costs for males and females respectively. The total gross energy requirements of the population was  $1.24 \times 10^9$  MJ or  $17.2 \times 10^3$  MJ *per*

*capita*. The total biomass of fish and squid prey consumed annually by the population was  $311 \times 10^3$  tonnes. The population consumed about 34% of prey from the Kerguelen Plateau including  $23.8 \times 10^3$  tonnes of the commercially targeted *Dissostichus eleginoides*. This suggests potential for competition between commercial fisheries and the southern elephant seal population at Heard Island.

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# CHAPTER 1

## GENERAL INTRODUCTION

### 1.1 INTRODUCTION

The southern elephant seal, *Mirounga leonina*, is one of the more abundant seal species in the world (Laws 1994), and as such is one of the major consumers of squid and fish in the Southern Ocean ecosystem (Laws 1977, McCann 1985, Boyd *et al.* 1994). The annual cycle of the southern elephant seal involves two periods at sea that are punctuated by two periods ashore, one for activities associated with reproduction, and the other for the moult. Some aspects of the terrestrial phase of their life cycle have been studied in detail, and elephant seals have been the subjects of studies investigating their ecology (Carrick and Ingham 1960, Bester and Wilkinson 1994), behaviour (McCann 1981, 1982), development (Bryden 1969, Guinet 1991), and energetics (Boyd *et al.* 1993, Fedak *et al.* 1994, Hindell and Slip 1997). Since 1987, the availability of archival and satellite linked recording devices has increased the number of studies concerned with the marine phase of the annual cycle of the elephant seal. These studies have provided information on the dive behaviour, and the movement patterns of elephant seals from Macquarie Island (Hindell *et al.* 1991a, 1991b, Slip *et al.* 1994), Marion Island (Bester and Pansegrouw 1992, Jonker and Bester 1994), South Georgia (Boyd and Arnborn 1991, McConnell *et al.* 1992, McConnell and Fedak 1996), and Patagonia (Campagna *et al.* 1995).

The population at Heard Island has received little study. A decline in the population from 1949 to 1985 has been reported (Burton 1986), but any attempts at explaining this decline (e.g. Hindell *et al.* 1994a) have relied largely on information gained from studying other populations. An activity that may impact on the elephant seal population at Heard Island is commercial fishing which has recently begun in the 200 nautical mile Australian Fishing Zone that surrounds Heard Island. Commercial fishing has occurred on the plateau surrounding Îles Kerguelen with substantial catches taken by Soviet, French and Ukrainian

vessels since the early 1970s (Williams and de la Mare 1995). Fishing was intensive and largely unregulated from 1970 to 1978 and stocks of some fish species on the Kerguelen shelf have been seriously depleted (Duhamel and Hureau 1990), and it has been suggested that the slow population growth of fish predators, such as fur seals, around Îles Kerguelen may be due to inadequate fish stocks (Bester and Roux 1986). A 200 nautical mile Economic Exclusion Zone was declared around Heard Island in 1979 and the only recorded fishing in this area was some exploratory Polish fishing in 1975 and a possible proportion of the Soviet catch in the early 1970s (Williams and de la Mare 1995). The potential effect of the Kerguelen Plateau fishery on the elephant seal population at Heard Island is uncertain as it has been found in studies of other populations that a large proportion of the population feeds a long way from their sub-Antarctic islands (Slip *et al.* 1994, McConnell and Fedak 1996). However, if elephant seals from Heard Island spend a significant amount of time within the fisheries zone, and if commercial fish species are an important component of elephant seal diet, then there may be potential for significant impact on the elephant seal population.

## 1.2 Biology of the Southern Elephant Seal

The southern elephant seal, *M. leonina* is the largest species of the world's 34 extant species of pinnipeds (King 1983). The species is highly sexually dimorphic. Reproductive adult males can be over 5 metres in length and weigh between 1,500 and 3,000 kg, with maximum mass reaching 3700 kg (Ling and Bryden 1981), while adult females range widely in mass from 350 to 800 kg (soon after giving birth) with most between 400 and 600 kg (Fedak *et al.* 1994). Mean pup mass at birth ranges between 34 and 49 kg, and mean pup mass at weaning varies between 98 and 171 kg depending on sex and location (SCAR 1991). The lactation period also varies among populations ranging from about 21 to 24 days (SCAR 1991). The mass of pups at weaning depends largely on the mass of the mother at the start of the breeding season (Fedak *et al.* 1996). Once pups are weaned they stay on shore fasting for

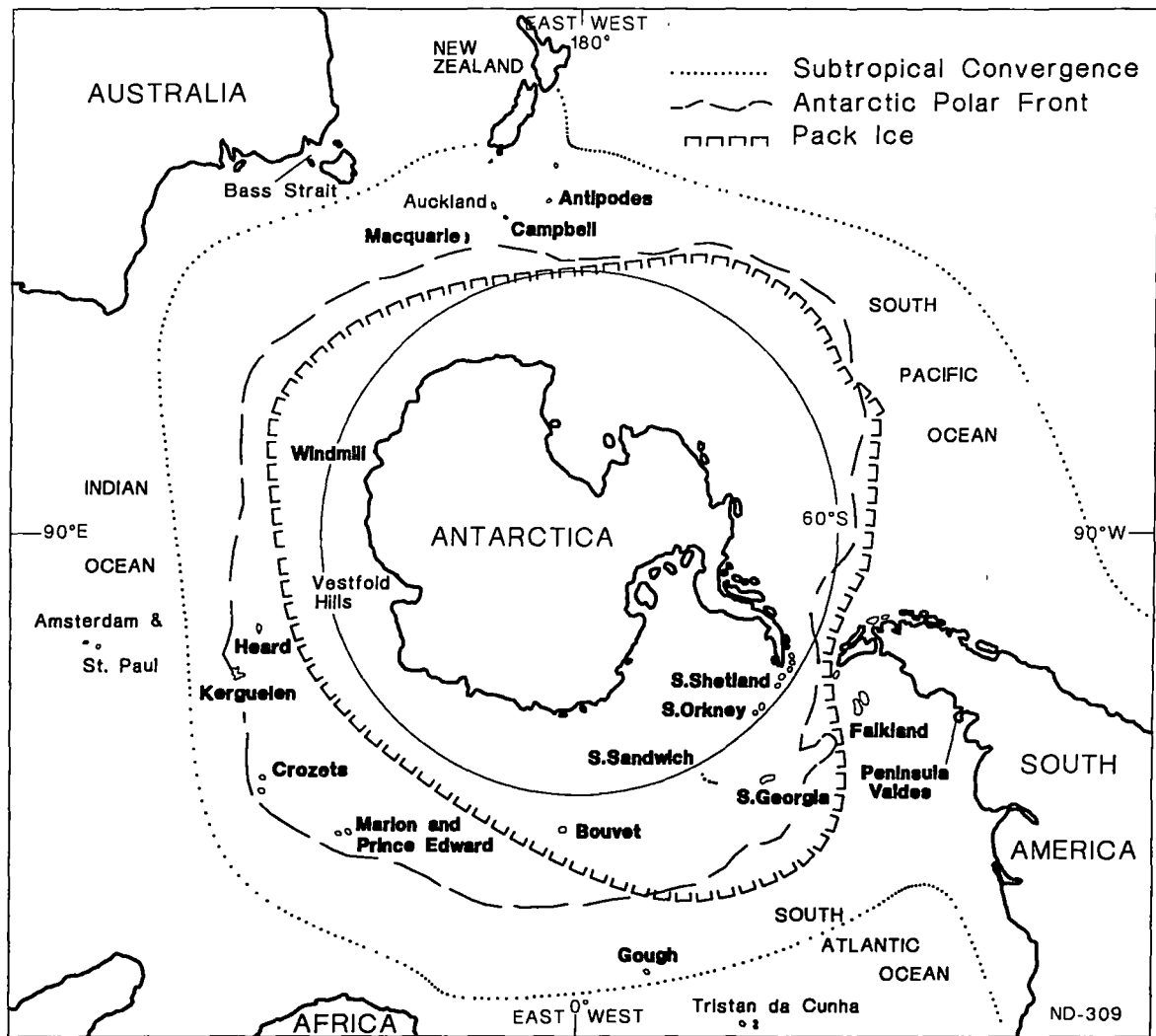
about 9 weeks, leaving their natal islands when their mass reaches about 68 - 70% of their weaned mass (Wilkinson and Bester 1990, Arnborn *et al.* 1993).

### 1.3 Distribution of Southern Elephant Seal Populations

The southern elephant seal has a circumpolar distribution and breeds mainly on sub-Antarctic islands that are close to the Antarctic Polar Front (Laws 1994). Laws (1960) defined three main southern elephant seal stocks: the South Georgia stock, the Macquarie Island stock, and the Kerguelen stock. The location of the main breeding colonies are shown in Fig. 1.1. The South Georgia stock is the largest numerically accounting for over half of the world population, and includes breeding colonies in the Scotia arc (South Georgia, South Orkney Islands, South Shetland Islands, South Sandwich Islands), together with Gough and Bouvet Islands (Laws 1994). While Laws (1960) included the populations from the Falkland Islands and South America in this stock, Laws (1994) suggested that on the basis of observed movements between these two breeding colonies and the lack of movements among other populations, that these populations may constitute a fourth elephant seal stock (Lewis *et al.* 1996). Recent studies of mitochondrial DNA also suggested that the South American group was separate from the South Georgia stock (Slade 1997). The Kerguelen stock includes Kerguelen and Heard islands, Marion and Prince Edward islands, and Îles Crozet, and the Macquarie stock includes Macquarie Island, Campbell Island, the Auckland Islands, and the Antipodes Islands (Laws 1994). Genetic studies using allozyme data showed that the populations on Heard Island and Macquarie Island have diverged genetically and could be considered distinct populations (Gales *et al.* 1989). Limited overlap of the two populations occurs on the Antarctic continent as adult males tagged at the Windmill Islands have been resighted at Heard Island, Îles Kerguelen, and Macquarie Island.

### 1.4 Distribution at Sea

Southern elephant seals dive almost continuously while at sea, diving deeply, and travelling long distances away from their breeding islands (Hindell *et al.* 1991a, 1991b,



**Fig. 1.1:** Map of the Southern Ocean showing the location of southern elephant seal breeding sites (bold), the average extent of pack ice, the Antarctic Polar Front, and the Subtropical Convergence.

Boyd and Arnborn 1991, Bester and Pansegrouw 1992, McConnell *et al.* 1992, McConnell and Fedak 1996). Adult seals travel long distances for prolonged periods at speeds of around 70 - 80 km/day, interrupted by periods where they are relatively stationary (McConnell and Fedak 1996). Because of their ability to travel large distances, vast areas of the Southern Ocean are available to elephant seals. Seals may use static physical features that are associated with high densities of prey, such as the continental shelf break, in order to locate prey (McConnell *et al.* 1996), as this strategy may prove more productive than pelagic meandering (McConnell *et al.* 1992). The oceanographic features around the main elephant seal breeding islands are slightly different. For example, Macquarie Island is on a mid-ocean ridge with very little shelf area, South Georgia has more shelf area and is relatively close to the Antarctic Peninsula, and Heard Island is on the Kerguelen Plateau (Gordon and Molinelli 1982). These differences suggest that elephant seals from each of these islands may have some differences in their movement patterns.

### **1.5 Past and Present Status of Elephant Seal Populations**

Most southern elephant seal populations were harvested for their oil at some time in the eighteenth, nineteenth and early twentieth centuries (Busch 1985). The extent and timing of sealing differed among populations. By the early 1800's the species was completely eliminated from the Bass Strait islands of southern Australia (Carrick and Ingham 1962a), while the Macquarie Island population was exploited from 1810 until 1919 (Cumpston 1968), and sealing occurred at Heard Island from 1855 to 1881 (Downes 1996). South Georgia was visited by sealers before 1800, and sealing occurred there in the nineteenth century (Busch 1985), then in the twentieth century sealing occurred there under licence from 1910 to 1964 (Laws 1994). The extent and the impact of the unregulated sealing is unknown but has been estimated from shipping logs to have been severe, with the population at Macquarie Island reduced by about 70%, although it was thought to have recovered to near pre-sealing levels by the 1900's (Hindell and Burton 1988a).

Since the 1950's there have been reports of serious declines in several southern elephant seal populations, including Macquarie Island (Hindell and Burton 1987), Îles Kerguelen (Pascal 1985, Guinet *et al.* 1992), Îles Crozet (Guinet *et al.* 1992), Marion Island (Wilkinson 1992), and Heard Island (Burton 1986). The extent of these declines was quite severe with some populations being reduced by over 50%. Several hypotheses have been proposed to explain the decline and a review of these can be found in Hindell *et al.* (1994a). However, while the Indian Ocean and Pacific Ocean populations have been declining, the South Georgia population appears to have been stable (Boyd *et al.* 1996), while the population at Peninsula Valdez, on the South American mainland has increased (Campagna and Lewis 1992).

Since 1984 the decline has stabilised at Heard Island (this volume, chapter 3) and Îles Kerguelen, but has continued to decrease at Îles Crozet (Guinet *et al.* 1992), Marion Island (Wilkinson 1992), and Macquarie Island (Slip, unpublished data). Table 1.1 summarises the current status of the main elephant seal breeding populations. The populations are presented in terms of pup production. In order to estimate total population size these numbers must be multiplied by a factor that is dependent on the age structure of the populations. For stable populations a multiplier of 3.5 gives an estimate of the total number of seals in the population aged one year and above (Laws 1994).

## 1.6 Thesis Structure and Aims

This study investigates the foraging ecology of southern elephant seals at Heard Island. It aims to further our understanding of how the southern elephant seal uses the marine resources of the Southern Ocean ecosystem, both spatially and temporally, and how changes in the population might occur. In order to study the at sea phase of the seals life cycle it is necessary to be able to immobilise animals safely and effectively. Chapter 2 describes a method for immobilising small southern elephant seals that is safe for both researcher and for

**Table 1.1:** Estimates of the size, status, and annual rates of change (%) of the major southern elephant seal populations within the four main stock groups.

Stock	Location	Pup Production		Population status		Rate of Change	Source
		Total	Year	Trend	Period		
South Georgia	South Georgia	113,444	1995	Stable	1985-95	0.0	Boyd <i>et al.</i> 1996
	South Orkney Islands	~ 5	1980s	Decreasing	1970's-80's	?	Laws 1994
	South Shetland Islands	689	1988	Decreasing	1980-88	-4.2	Vergani & Stanganelli 1990
	Gough Island	28	1989	Stable	1973-89	0.0	Bester 1990
Patagonia	Peninsula Valdez	9,636	1990	Increasing	1969-90	3.2	Campagna & Lewis 1992
	Falkland Islands	~ 1,000	1960	Uncertain		?	Laws 1960
Kerguelen	Îles Kerguelen	45,000	1977	Decreased	1970-77	-4.8	van Aarde 1980
	Îles Kerguelen	41,100	1989	Stable	1984-89	0.0	Guinet <i>et al.</i> 1992
	Heard Island	16,400	1985	Decreased	1949-85	-1.9	This volume, Chapter 3
	Heard Island	17,600	1992	Stable	1985-92	0.0	This volume, Chapter 3
	Marion Island	585	1989	Decreasing	1951-89	-4.8	Wilkinson 1992
	Prince Edward Island	411	1977	Uncertain		?	Condy 1978
	Îles Crozet	612	1989	Decreasing	1966-89	-5.7	Barrat & Mougine 1978, Guinet <i>et al.</i> 1992
Macquarie	Macquarie Island	24,000	1985	Decreasing	1949-85	-2.1	Hindell and Burton 1987
	Macquarie Island	21,000	1996	Decreasing	1985-96	-1.2	Slip, unpublished data
	Antipodes Island	113	1978	Uncertain		?	Taylor and Taylor 1989
	Campbell Island	5	1986	Decreasing	1947-86	-8.6	Taylor and Taylor 1989
World Total		195,592					



the seal, and relatively quick. This method also has implications for working with larger seals. Chapter 3 discusses the present status of the Heard Island population and describes the annual cycle for different age classes of the population. This chapter looks at population trends over the past 10 years and re-analyses the population estimates from the early 1950s to examine past population trends. The haulout patterns are described for the Heard Island population to compare them with other populations and to evaluate the possibility of using counts of sections of the population other than breeding cows, as indicators of population trends, given that Heard Island is rarely visited during the elephant seal breeding season. Chapter 4 identifies the major prey species in the diet of elephant seals at Heard Island, and examines differences by age class, sex, and season. The composition of the cephalopod portion of the diet is compared with that of other predators of the Southern Ocean ecosystem. Chapter 5 looks at the foraging behaviour of adult male and adult female elephant seals, identifies the location of the main foraging areas, and looks at the relationship between dive behaviour and sea temperature and bathymetry. Chapter 6 examines the diving behaviour of juvenile seals and estimates the location of their main foraging grounds. Chapter 7 synthesizes the information from the previous four chapters, and uses information from the literature to develop a bioenergetic model of food consumption for the Heard Island elephant seal population.

The chapters of this thesis have been prepared as separate papers, and this has led to a certain amount of repetition in the methods section of some of the chapters. Chapters 2, 4, and 6 have been published previously and the citations for these along with any co-authors, are credited in footnotes at the beginning of each chapter. These chapters are presented without their abstracts and references which have been incorporated into the abstract and references of the complete thesis. I was always the senior author and took full responsibility for data collection, analysis, and presentation. The field work was conducted on Heard Island from January 1992 until March 1993.

## CHAPTER 2

### INTRAMUSCULAR AND INTRAVENOUS IMMOBILISATION OF JUVENILE SOUTHERN ELEPHANT SEALS<sup>1</sup>

#### 2.1 INTRODUCTION

Studies of wild populations of seals often require them to be restrained in order to perform tasks such as blood sampling, weighing, collecting stomach contents, and attaching electronic recording devices. Some pinnipeds are difficult to immobilise, and unpredictable responses to intramuscular administration of a variety of anaesthetic drugs have been reported (Geraci 1973, Parry *et al.* 1981, Erickson and Bester 1993). Pinnipeds have physiological adaptations that allow them to dive for long periods, and survive in a cold environment, thus apnoea and hyperthermia are common side effects of immobilisation (Vergani 1985, Mitchell and Burton 1991).

Southern elephant seals have often been immobilised with intramuscular injections of cyclohexamine based anaesthetic drug combinations such as tiletamine-zolazepam or ketamine-diazepam (Gales 1989, Baker *et al.* 1988, 1990, Mitchell and Burton 1991). Drugs have been administered intramuscularly because the animals are large, potentially dangerous, and in most cases, cannot be physically restrained to allow intravenous access before drug administration (Gales 1989). In phocid seals the size and position of the extradural vein (King 1983), makes the task of gaining intravenous access relatively easy, provided the animal can be manually restrained first (Geraci and Sweeney 1978). Veterinary studies of domestic animals have shown that intravenous drug administration offers advantages over intramuscular administration in that the onset of action is more rapid and drugs can be administered to effect the desired level of immobilisation (Booth and McDonald 1982).

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Nonetheless, few investigators have immobilised wild seals using only intravenously administered drugs (Engelhardt 1977), and some have actively avoided using this route (Gales and Burton 1987).

Here I describe a method for induction of anaesthesia in small (less than 3 yr) southern elephant seals using intravenous drug administration. I theorised that by physically restraining the animals and administering the drugs intravenously, the dose of anaesthetic could be decreased and a more predictable response achieved than when intramuscular drug administration was used. I compared this method of intravenous administration with intramuscular drug administration in yearlings and juveniles of this species, in order to suggest which might be better under field conditions. During the study some animals became apnoeic and I examined the relation between the duration of apnoea and the theoretical aerobic dive limit (Kooyman 1989).

## 2.2 STUDY AREA AND METHODS

During July and August 1992, I sedated 32 juvenile (8 - 10-month-old pups of the yr and 20 - 22-month-old yearlings, 22 M and 10 F) southern elephant seals at Heard Island, Southern Ocean (53° 05' S, 73° 30' E) with a mixture of ketamine hydrochloride (186 mg/mL, Parke Davis, Sydney, Australia) and diazepam (5 mg/mL, Valium<sup>®</sup>, Roche Products, Pty Ltd, Sydney, Australia). I estimated body mass by eye, then injected a volume of drug such that the estimated dose rates were 2.0 - 3.0 mg/kg of ketamine (2 - 3 mL), and 0.05 - 0.2 mg/kg of diazepam (2 - 4 mL), chosen from past experience. Before injecting the drugs I manually restrained each seal by placing a reinforced canvas bag (1 m in diameter and 1.5 m deep) over its head and sitting on its back. I then inserted an 18 g, 90-mm-spinal needle into the extradural intravertebral vein in the posterior lumbar region, and slowly administered a dose of diazepam, followed immediately by ketamine, with the intention of inducing sufficient immobilisation to allow stomach flushing. Complete administration of drugs took

between 1 and 2 minutes. I assessed the depth of anaesthesia on an 8-point scale ranging from 1 (light sedation) which was characterised by a general slowing of behavioural responses, to 8 (deep anaesthesia) characterised by little or no palpebral response and complete loss of muscle tone (Woods *et al.* 1994). To proceed with the stomach flushing, a depth of at least 5 (heavy immobilisation) was required, which was characterised by a moderate palpebral response with the animal unable to withdraw its head from a stimulus, although the eyes followed objects passing in the animal's field of vision. Muscle tone was slight, but animals could easily be rolled over.

To compare the dose of ketamine and the duration of immobilisation between intravenously and intramuscularly administered drugs, I compared the Heard Island animals with a dataset from 21 juvenile (11 - 13 month-old yearlings and 2 year olds, 13 M and 9 F) southern elephant seals, which were chemically immobilised with intramuscular injections of ketamine and diazepam at Macquarie Island, Southern Ocean (54° 30' S, 157° 0' E) in November 1989. These drugs were administered by remote injection (Ryding 1982), using a 1.5-m plastic tube and an 18 g, 90-mm-spinal needle into the muscles of the lateral posterior lumbar region. Body mass was estimated and a volume of drugs was injected such that estimated dose rate was between 3.0 and 6.0 mg/kg for ketamine and 0.05 to 0.2 mg/kg for diazepam. These animals were immobilised for the purpose of stomach flushing. A depth of anaesthesia of at least 5 was required, and dose rates were kept to the minimum to achieve this level. Both groups were monitored similarly, and I calculated actual dose rates after animals were weighed using a sling and tripod. I tagged each seal in its hind flippers with plastic Jumbo Rototags (Dalton Supplies, Woolgoolga, N.S.W., Australia).

I followed the degree and time course of the chemical restraint from injection until total recovery, and I recorded the duration of any episodes of apnoea. I defined induction time as the time of injection until the animal ceased to struggle, and duration of chemical restraint from the time of induction until the animal regained awareness, could raise its head,

and respond to surrounding stimuli (recovery). When animals responded aggressively to our approach in a manner that was similar to the response of an unrestrained animal, I ceased observation and allowed the animal to move away. When apnoea occurred in animals from the intravenous group, and persisted for more than 5 minutes (periods of apnoea less than 5 min were regarded as common and are often observed in sleeping juvenile seals [personal observation]), I observed animals closely and monitored strength of capillary refill by applying finger pressure to the gums, and I noted any cyanotic change in the gums. I kept an endotracheal tube, oxygen, and the respiratory stimulant doxapram (Bomac Laboratories, Castle Hill, N.S.W., Australia) on hand to initiate emergency procedures in the event of severe cyanosis and weak capillary refill (Woods *et al.* 1994). I did not include animals which became apnoeic after intramuscular administration in the dataset as they were immediately intubated and given oxygen and doxapram until they showed signs of breathing unassisted.

I examined the relation between the theoretical aerobic dive limit (ADL) and the duration of apnoea for seals which received intravenous drugs and became apnoeic. For each apnoeic animal, I calculated ADL from the equation:

$$\text{ADL} = (\text{lean mass} \times \text{T O}_2) / \text{RMR},$$

where T O<sub>2</sub> (total available oxygen) = 0.079 l O<sub>2</sub> /kg (Kooyman 1989),

RMR (resting metabolic rate) = 0.0113 (lean mass<sup>0.75</sup>) l O<sub>2</sub> /minute (Schmidt-Nielsen 1983),

and lean body mass = 0.75 x total body mass (Slip *et al.* 1992a).

Statistical analyses follow Zar (1984), and values are presented as mean  $\pm$  standard deviation. I tested for homogeneity of variance using the variance ratio test, and data were log transformed if variances were heteroscedastic. I used multiple regression analysis using

intravenous dose and intramuscular dose as treatments with duration of immobilisation as the dependent variable to test for any dose response relations.

## 2.3 RESULTS

The reaction of seals to physical restraint differed among individuals; some were quiet, calm and easily restrained while others reacted vigorously and were difficult to get in the canvas bag. Once the head bag was in place, the animal could be restrained effectively by 1 person sitting on the back of the seal. All animals resisted physical restraint until chemical restraint began to take effect.

Thirty of 32 animals injected intravenously became heavily immobilised (level 5) and only 2 animals responded to the drugs more deeply than this. These 2 animals became lightly anaesthetised (level 6 - Woods *et al.* 1994). All animals moved away, usually towards the water, within 10 minutes of recovery. When I located animals 1 to 2 hours later, their behaviour was indistinguishable from seals which had not been immobilised. I located all animals at least 3 days after immobilisation and no animals died or showed ill effects as a result of the procedures.

There was no relation between the amount of drug injected (dose) and duration of immobilisation for either the intramuscular or the intravenous treatments (multiple regression,  $F_{1,49} = 0.74$ ,  $P = 0.39$ ), with the only significant factor being the treatments ( $F_{1,50} = 12.43$ ,  $P < 0.001$ ). The mean dose of diazepam was not different between the 2 groups ( $t = 1.89$ ,  $\nu = 51$ ,  $P = 0.07$ ), but the mean dose of ketamine was lower for intravenous administered ketamine ( $t = 16.99$ ,  $\nu = 51$ ,  $P < 0.001$ , Table 2.1). In addition, ketamine doses were less variable when intravenous administration was used (variance ratio test,  $F_{20,31} = 7.42$ ,  $P < 0.001$ ). Mean time to induction was lower ( $t = 4.94$ ,  $\nu = 51$ ,  $P < 0.001$ ), and less variable ( $F_{20,31} = 29.65$ ,  $P < 0.001$ ) with intravenous administration. Mean duration of immobilisation was also shorter ( $t = 3.53$ ,  $\nu = 50$ ,  $P < 0.001$ ), and less variable ( $F_{20,30} = 3.04$ ,

**Table 2.1:** Mean ( $\pm$  *sd*) mass (kg), dose rates of ketamine and diazepam (mg/kg), mean time to immobilisation (min), and mean duration of immobilisation (min) for southern elephant seals with intramuscular administration and intravenous administration of immobilising drugs at Macquarie and Heard Islands in 1989 and 1992 respectively. Ranges are given in parentheses. Significance was tested by 2 sample *t*-test assuming equal variance.

	Macquarie Island	Heard Island	Significance
	Intramuscular	Intravenous	
Mass (kg)	192 $\pm$ 57.6 (128 - 350)	178 $\pm$ 45.2 (109 - 263)	$P = 0.20$
Dose of ketamine (mg/kg)	6.22 $\pm$ 1.13 (4.36 - 8.57)	2.50 $\pm$ 0.44 (1.81 - 3.40)	$P < 0.001$
Dose of diazepam (mg/kg)	0.087 $\pm$ 0.035 (0.035 - 0.1292)	0.106 $\pm$ 0.038 (0.040 - 0.183)	$P = 0.07$
Time to induction (min)	7.05 $\pm$ 5.77 (1 - 23)	1.91 $\pm$ 1.01 (1 - 7)	$P < 0.001$
Duration of immobilisation (min)	49.6 $\pm$ 18.79 (22 - 94)	35.1 $\pm$ 10.78 (17 - 59)	$P = 0.0001$
<i>N</i>	22	32	



$P < 0.003$ ) with intravenous injection. With these dose rates the guaranteed minimum duration of immobilisation (where 95% of seals were still immobilised) was 18.8 minutes for intramuscular drugs, and 17.4 minutes for intravenous drugs. With intravenous injection 8 of 32 seals (25%) were apnoeic for more than 5 minutes. Those apneas ranged from 8 to 20 minutes, and averaged  $16 \pm 4.5$  minutes. During apnoea, mucous membrane colour remained pink, capillary refill was rapid in all cases, and animals resumed breathing without treatment and recovered uneventfully. There was no difference in dose rate of ketamine ( $t = 1.33$ ,  $\nu = 28$ ,  $P = 0.19$ ), dose rate of diazepam ( $t = 0.16$ ,  $\nu = 28$ ,  $P = 0.88$ ) or duration of immobilisation ( $t = 1.01$ ,  $\nu = 27$ ,  $P = 0.32$ ) between those animals that became apnoeic, and those that did not. The duration of apnoea was always less than the calculated theoretical aerobic dive limit (Table 2.2). With intramuscular injection, 6 of 27 seals (22%) were apnoeic for more than 5 minutes. The duration of apnoea was not measured as these animals were immediately intubated and artificially respirated.

## 2.4 DISCUSSION

Intravenous administration of injectable anaesthetic agents to immobilise southern elephant seals had advantages over intramuscular administration of shorter and less variable induction time, and shorter and less variable duration of immobilisation (Table 2.1). In addition, intravenous injection achieved the same level of immobilisation with lower and less variable dose rates than intramuscular injection. The wide variation of response to intramuscular administration suggests that in some cases part or all of the drug dose may have been accidentally injected intravenously, despite care taken to avoid this occurring. Degree of fatness could have been responsible for some of the variability of response as animals in their first year are highly variable in condition (Australian Ant. Div., unpublished data). The major advantage of direct intravenous injection is that because of the short induction time, drugs can be administered to effect the required level of immobilisation.

**Table 2.2:** Dose rate of ketamine and diazepam (mg/kg), time to induction and duration of immobilisation (min), duration of apnoea (min) and estimated aerobic dive limit (ADL) for southern elephant seals where apnoea occurred following intravenous administration of immobilising drugs at Heard Island in 1992.

Mass (kg)	Dose of ketamine (mg/kg)	Dose of diazepam (mg/kg)	Induction time (min)	Duration time (min)	Duration of apnoea (min)	Aerobic dive limit (ADL) (min)
257	2.17	0.08	2	28	20	26.0
155	2.40	0.13	2	45	20	23.0
257	1.81	0.08	2	27	19	26.0
167	2.23	0.12	2	42	12	23.4
174	2.14	0.12	2	40	8	23.6
223	2.50	0.09	1	33	14	25.1
121	3.08	0.17	1		15	25.6
232	2.40	0.09	1	50	20	25.4
Mean $\pm$ sd	$2.34 \pm 0.37$	$0.11 \pm 0.03$	$1.63 \pm 0.56$	$37.9 \pm 8.75$	$16 \pm 4.5$	$24.3 \pm 1.6$

Dose of ketamine was not related to the time to recovery in this study. However, Engelhardt (1977) found that dose rate of ketamine given intravenously to wild harp seal pups correlated well with duration of immobilisation. The pups in that study were of similar age and condition, and dose rates ranged from 0.5 to 11.1 mg/kg. The lack of a direct relation between dose and duration of immobilisation seen in the present study may be due to individual differences among animals such as size, condition, absorptive state, or the level of excitement immediately before injection, or may simply be due to the small range of dose rates (1.81 - 3.40 mg/kg) used in this study. The absence of a relation in the intramuscular group, where doses ranged from 4.36 to 8.57 mg/kg highlights the variable responses of this group. The lack of a direct relationship between dose rate and duration of immobilisation with intravenous drug delivery has also been reported by other workers (e.g. Bester 1988a).

Minimising the time an animal is immobilised, is often desirable, e.g. where immobilised animals must be protected from aggressive reproductive males, where mother-pup pairs are separated during immobilisation, or where environmental conditions are hazardous, such as working on unstable pack ice. Although antagonists may prove effective in some cases, these have not yet been tested on southern elephant seals (Woods *et al.* 1994). The method described in this study, of physical restraint followed by intravenous administration of drugs, results in shorter duration of immobilisation and may have applications for use with other species, and with any drug that can be safely injected intravenously. If seals can be physically restrained with a minimum of stress to both the animals and the restrainers, and intravenous access can be easily and quickly achieved, then this method provides a more rapid and controlled technique for immobilising small phocid seals, than when drugs are administered intramuscularly. This method has the disadvantage that it may be more stressful. The relation between stress and apnoea has not been determined, although it has been suggested that fright could initiate a dive response (Backhouse 1964). A further disadvantage of intravenous injection is that under unsanitary

field conditions there is potential for the introduction of bacteria and other pathogens directly into a major part of the circulatory system. Also there is potential for serious damage to the large extradural vein especially with a struggling seal that is physically restrained. Thus, in some cases the advantages of lower dose rates, shorter durations, and more predictable apneas (see below) may be overridden by these disadvantages. If this is the case, then a better method of safe and predictable immobilisation might be to lightly sedate a seal with an intramuscular dose of ketamine alone, diazepam alone, or a combination, and then maintain immobilisation with the desired doses of drugs by intravenous injection, possibly with a catheter placement. This technique has worked well with larger southern elephant seals (Slip unpubl. data), and also has been used for northern elephant seals, *Mirounga angustirostris* (B. Stewart, Hubbs-Sea World Res. Inst., pers. comm.).

One of the major difficulties in chemically immobilising phocid seals is their tendency to undergo prolonged periods (10 min or more) of apnoea, as this makes monitoring the course of anaesthesia difficult, and if apnoea persists then fatalities may occur (Gales 1989, Mitchell and Burton 1991). What induces apnoea is unclear and it is difficult to predict when a seal will become apnoeic. In the present study the doses of intravenous ketamine administered to those animals that underwent apnoea did not differ from those that did not. There is some evidence to suggest that rapid intravenous drug administration may induce apnoea (Woods *et al.* 1994), and in the present study, drugs were injected slowly in an attempt to avoid this. Despite this precaution, 25% of animals became apnoeic, as did 22% of those injected intramuscularly.

Elephant seals undergo periods of apnoea of over 10 minutes when sleeping on land (Kenny 1979), and are capable of dives in excess of 100 minutes (Hindell *et al.* 1992). During dives elephant seals do not usually exceed ADL; adult males and post breeding adult females exceeded ADL on only 1 and 7% of dives respectively (Slip *et al.* 1994). Although physiological responses and oxygen distribution may be different during chemically induced

apneas than during dive or sleep apneas, the comparison between ADL and duration of apnoea (Table 2.2) suggests that if seals become apnoeic when immobilised with intravenous administration, they will usually begin to breath again before exceeding the ADL and incurring an oxygen debt. However, this is not always the case, particularly with intramuscular administration, and fatalities often have been reported in other studies, (Engelhardt 1977, Gales and Burton 1987, Baker *et al.* 1988, Woods *et al.* 1989, Mitchell and Burton 1991). Seals that undergo apneas in excess of their ADL sometimes survive (Slip pers. observ.), although some form of emergency procedure is often necessary, such as intubation (Baker *et al.* 1990).

The stimulation of apnoea may be related to the relative concentration of drugs in the blood, and apnoea may end when either the blood concentration of drug drops below a critical point, or when blood gas concentrations reach a point that stimulates breathing. Hammond and Elsner (1977) reported that seals always became apnoeic when anaesthetised, which suggests that prolonged apnoea may be related to the relative concentration of drugs in the blood. That animals in our study did not undergo apnoea in excess of the ADL suggests that either blood gas concentration is the most important stimulus to breathing and/or the concentration of drug had dropped below a critical level before the ADL was reached. When seals undergo apnoea, peripheral vasoconstriction may occur (Kooyman *et al.* 1981, Butler and Jones 1982). If drugs were administered via the intramuscular route, rate of drug absorption during apnoea may slow. When the animal resumes breathing and circulation to muscles improves, the drug may be released into the systemic circulation resulting in prolonged restraint, and possibly a further period of apnoea. Thus, apnoea may be less likely to cause complications when drugs are delivered intravenously than when they are administered intramuscularly.

### **2.4.1 Management Implications**

Southern elephant seal populations at Heard and Macquarie islands have declined by about 50% since the 1950s (Laws 1994). At Macquarie Island, this decline has been due largely to increases in mortality of animals during their first year at sea, and changes in the distribution and abundance of their prey may be a proximate cause of this mortality (Hindell 1991). To determine how changes in food availability affect demography, studies of the diet and foraging behaviour with procedures such as stomach flushing, or the attachment of electronic recorders are necessary. These procedures in turn require a safe and rapid method of immobilisation. I suggest that for pups of the year, yearling, and 2-year old southern elephant seals, manual restraint and intravenous injection of drugs by a suitably trained operator provides a safer, faster, and more predictable method of immobilisation than intramuscular injection.

## **2.5 ACKNOWLEDGEMENTS**

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# CHAPTER 3

## POPULATION STATUS AND SEASONAL HAULOUT PATTERNS OF THE SOUTHERN ELEPHANT SEAL (*MIROUNGA LEONINA*) AT HEARD ISLAND

### 3.1 INTRODUCTION

The world population of southern elephant seals is recognised as being composed of four stock groups: South Georgia, Peninsula Valdez and the Falkland Islands; Macquarie Island, and Îles Kerguelen which includes Heard Island, Îles Crozet and Marion Island (Laws 1994). While the South Georgia population has remained stable over the past 45 years (Boyd *et al.* 1996), serious declines have been reported for the Macquarie population (Hindell and Burton 1987), and the Kerguelen population has been declining at several locations including Heard Island (Burton 1986), Marion Island (Wilkinson and Bester 1988), Îles Crozet (Barrat and Mougins 1978, Guinet *et al.* 1992), and Îles Kerguelen (van Aarde 1980, Pascal 1981). The decline at Heard and at Macquarie Islands were long-term declines occurring between 1959 and 1985 for Macquarie Island and between 1949 and 1985 at Heard Island. Since 1985 the rate of decline at Macquarie Island has reduced from about 2.1% to 1.6% per year (unpubl. data), the population at Îles Kerguelen has been stable from 1985-89 (Guinet *et al.* 1992), the population at Îles Crozet has declined at 5.7% per year from 1980-89 (Guinet *et al.* 1992), and the population at Marion Island has declined by 1.9% annually from 1983-1989 (Bester and Wilkinson 1994).

The southern elephant seal has a consistent and predictable annual haulout pattern which has been described at Macquarie Island (Carrick *et al.* 1962, Hindell and Burton 1988b), Signy Island (Laws 1956), and Marion Island (Condy 1979). Despite the predictability of these haulouts there have been few attempts at describing the annual haulouts and these have largely concentrated on the haulout of breeding females (Pascal

1979, 1981, 1985, van Aarde 1980, Hindell and Burton 1987, 1988b, Rothery and McCann 1987). Most of the above studies have concentrated on describing the adult female haulout pattern during the breeding season using several mathematical models. Rothery and McCann (1987) modelled the haulout process of breeding females based on empirical observations of maternal time budgets during lactation. Only Hindell and Burton (1988b) have tried to describe all the annual haulouts mathematically to enable predictions to be made of maximum numbers ashore from incomplete data. As Heard Island is remote and infrequently visited, the timing of visits there do not always correspond to the peak of breeding haulout. If other haulouts can be mathematically described then these may be useful as indicators of population change.

The objectives of this study were: (1) to determine the status of the Heard Island population; (2) to describe the annual haulout process there to assess the potential of using these haulout patterns to examine inter-annual variation (3) to reanalyse the results from earlier surveys using population models that are based on more recent knowledge of the biology of southern elephant seals in order to determine the magnitude of the decline and the current population trends, and (4) to review the potential causes of population trends in the Indian Ocean.

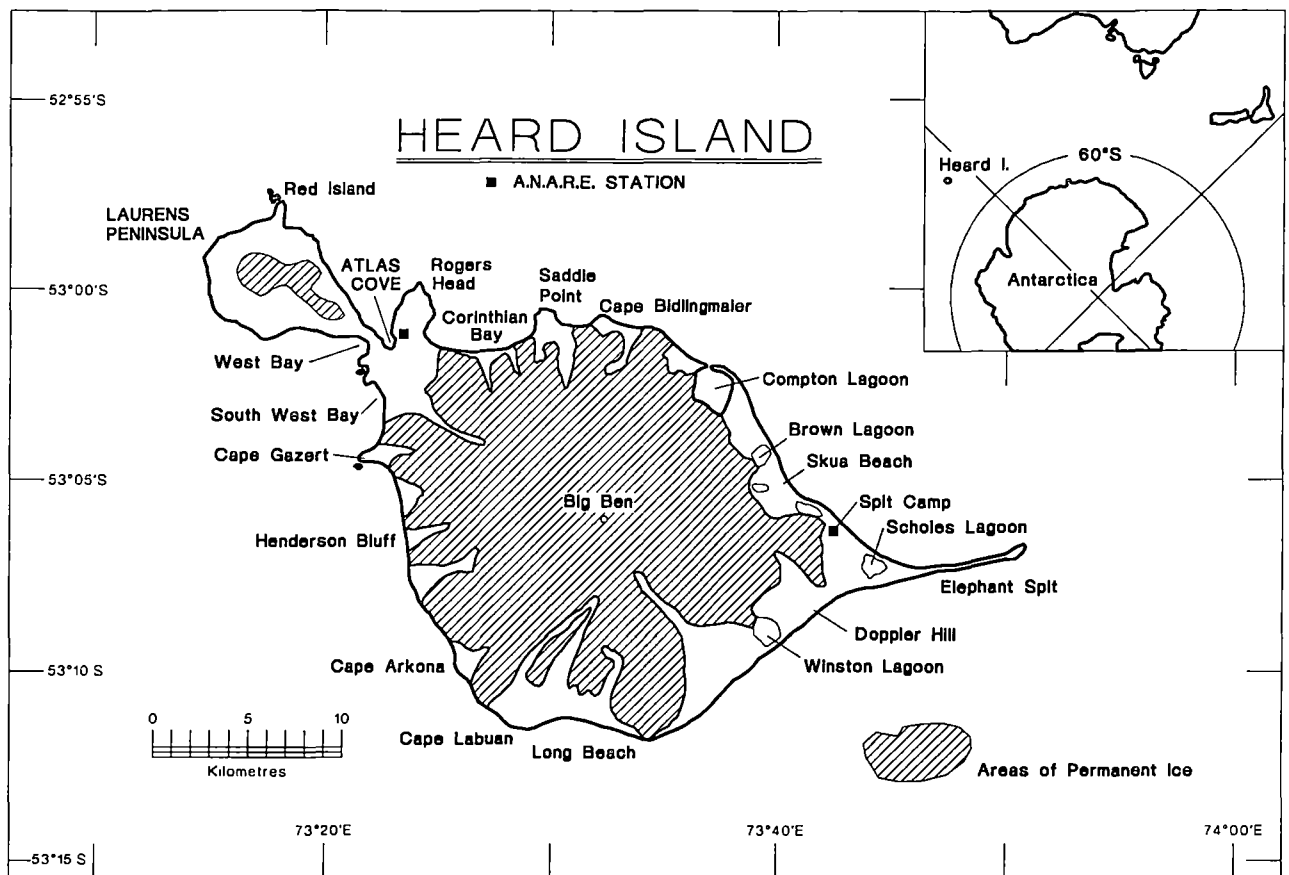
## **3.2 MATERIALS AND METHODS**

### **3.2.1 Counting Procedures**

#### **3.2.1.1 Haulout Patterns**

From February 1992 until March 1993 I counted, on average once per week, elephant seals which were hauled out in a triangular area bounded by Spit Camp, the western shore of Scholes Lagoon, and Doppler Hill (Fig. 3.1). I counted animals according to the following classifications: adult male, sub-adult male (approximately 4 to 6 year-olds not much larger than adult females), adult female, juvenile (animals in their second and third year, sexes not distinguished), and underyearlings (animals in their first year). These classifications were





**Fig. 3.1:** Map of Heard Island showing location of major landmarks. Elephant seals haul out at the eastern end of the island from Long Beach to Compton Lagoon, and at the western end of the island on the north coast from Red Island to Saddle Point, and on the south coast from West Bay to Cape Gazert. The breeding season serial counting area was from Spit Bay to the beginning of Elephant Spit and back to Doppler Hill.

estimated from recorded lengths of known age animals (Australian Antarctic Division, unpublished data). I counted all seals ashore at the eastern end of Heard Island, referred to as the Spit Bay area and including Long Beach to Compton Lagoon, three times outside of the breeding season to determine the proportion of the population of juvenile seals represented by the weekly counts. These counts were in March, June, and December.

### 3.2.1.2 Population Status

From September 1 1992 I counted seals from Spit Camp along the northern side of Scholes Lagoon to the point where the Spit was regularly breached, then along the south side of Scholes Lagoon to Doppler Hill. Serial counts were made of the females constituting each harem 56 times between September 1, and November 16, and counts were made almost daily from 30th September until 24th October. Dead pups were noted and weaned pups were counted until 10 days after the peak of adult female haulout. Males were counted about twice per week for the duration of the breeding season.

I chose adult females as the major unit for counting rather than pups as it possible to obtain an accurate census of adult females, and the time they spend ashore can be quantified. Pups are difficult to count with the same accuracy because their smaller size often means they are obscured from view, and at the peak of the breeding season pups can vary in mass about eight fold which makes counting difficult. Counts were recorded at the level of the group or harem. Each harem was counted twice and if these counts differed by greater than 5% a third count was undertaken, and a mean of the two closest counts was used.

Because of the glaciated nature of Heard Island only the area east of Compton Lagoon and Long Beach was accessible during the 1992 elephant seal breeding season. However, this area includes 90 to 95% of the elephant seals on the island (Carrick and Ingham 1962b).

### 3.2.1.3 Past Status

There was a continuous Australian National Antarctic Research Expeditions (ANARE) presence on Heard Island from 1949 to 1954, with the centre of activity based at Atlas Cove, and summer ANARE from 1985-1987. From 1949 to 1952 serial counts of adult females and adult males were made on the four main beaches in the Atlas Cove area. Reliable whole island counts of elephant seals were completed in 1949 and 1987, and almost complete counts were made in 1950, 1951, and 1985. In 1985 and 1987 Elephant Spit was broken by a wave washed section about 2 km across which isolated the last 2 km of the spit and made it an island (Burton 1986). Aerial photographs were used to count the elephant seals on Spit Island in both years, and the counting method was checked against ground counts.

## 3.2.2 Analytical procedures

### 3.2.2.1 Population Status

I used two models to determine total number of adult females ashore or pup production from count data. These were the normal distribution model, and the Rothery and McCann (1987) model. The models have been used previously to determine the size of elephant seal populations, and each model has slightly different assumptions. The normal distribution model is a mathematical description of the haulout and has been used to determine the status of the elephant seal population at Macquarie Island (Hindell and Burton 1988b). These authors demonstrated that the haulout pattern of adult female elephant seals during the breeding season was highly predictable and could be described by stochastic models based on the normal (or Gaussian) distribution. The model assumed that the timing of the haulout of adult females was consistent over the whole of the island, and thus, the haulout peak could be determined from serial counts of a small sample of the population. The Rothery and McCann (1987) model was used by these authors and others (eg. Boyd *et al*

1996) to determine the status of the elephant seal population at South Georgia. This model was based on the haulout pattern and time ashore of adult females.

Serial counts of seals at Spit Bay (1992) or Atlas Cove (1949-1987) were fitted to a normal curve with mean  $\mu$ , measured in days from September 1, and standard deviation  $\sigma$  for each year, using a nonlinear least squares regression method based on the Levenberg-Marquardt algorithm (Press *et al.* 1988). Counts were expressed as a proportion of the maximum number ashore, and these proportions were used to correct raw counts covering all accessible parts of the island to determine the maximum cows ashore for the whole island. Serial counts of dead pups and weaned pups from 1992 and 1987 were used to determine the proportion of the population of adult females represented by the maximum number ashore at the peak, assuming that each dead pup and each weaned pup counted prior to the haulout peak represents an adult female that had already left the beach.

In 1985 and 1987 three counts were made of all seals apart from those on Spit Island. To estimate the island population these points were fitted to the normal distribution model with the date of maximum haulout  $\mu$  determined from the Atlas Cove distribution. In 1949 and 1950 whole island counts were made in the last week of October and the first week of November respectively. These counts were corrected using the curve fitted to the Atlas Cove haulout for each year. In 1951 the whole island count was carried out in late November and very few cows were present, but pups were counted. These counts were then corrected to give an estimate of adult females by displacing the curve determined from the Atlas Cove haulout forward by 25 days, and allowing for pre-weaning pup mortality of 2.5%.

The model of Rothery and McCann (1987) also assumes that adult females haul out following a normal distribution with mean  $\mu$ , measured in days, and standard deviation  $\sigma$ . It also assumes that all animals haul out for the same length of time  $S$ , which represents the duration of lactation plus the period between arrival and birth. If  $N_H$  is the size of the

population of adult females that haul out in a given area and  $n(t)$  adult females are counted at time  $t$ , then on average

$$n(t) = N_H p(t, \mu, \sigma, S) \quad (1)$$

where  $p(t, \mu, \sigma, S)$  is the expected proportion of cows hauled out at time  $t$  (Rothery and McCann 1987). For haulouts which are normally distributed

$$p(t, \mu, \sigma, S) = \Phi\{(t - \mu)/\sigma\} - \Phi\{(t - S - \mu)/\sigma\} \quad (2)$$

where  $\Phi$  is the cumulative distribution function of the standardised normal distribution (Rothery and McCann 1987). This equation is made up of two cumulative normal distribution functions, one which describes the arrival of adult females and one which describes the departure (see Boyd *et al.* 1996).

Equation (1) also represents a straight line relationship between  $n(t)$  and  $p(t, \mu, \sigma, S)$ , which has a slope equal to  $N_H$  (total size of the haulout population) and passes through the origin. Least squares estimates of  $\mu$  and  $\sigma$  which minimised the residual variation around the regression line were used.

The value of  $S$  was derived empirically. I determined length of lactation by tagging and weighing randomly selected pups with plastic Jumbo Rototags (Dalton Supplies, Woolgoolga, N.S.W., Australia) on the day of birth and checking them daily until they had weaned and their mothers had returned to sea. The mean time ashore between arrival and parturition was determined by marking adult females on their first day ashore and observing them daily until they were observed with a pup.

The error associated with estimating the total haulout from both the models was estimated by resampling the detailed serial count at Spit Bay randomly and without replication to simulate the results of seven censuses, with ten replicates. These replicates were then used to estimate the total haulout population using both the normal distribution model and the Rothery and McCann (1987) model.

The intrinsic rate of population change was calculated using the exponential function:

$$N_t = N_0 e^{rt} \quad (3)$$

where  $N_0$  = size of the original population

$N_t$  = population size at time  $t$

$r$  = exponential rate of population change

$t$  = time elapsed between the two determinants of population (Caughley 1977, Bester and Wilkinson 1994). Intrinsic rate of change was converted to an annual percentage change by:

$$\text{Annual percentage change} = (e^r - 1) * 100 \quad (4)$$

(Caughley 1977, Bester and Wilkinson 1994).

### 3.2.2.2 Haulout Patterns

Haulout data for each component of the population were fitted to the normal distribution function using a non-linear least squares regression method based on the Levenberg-Marquardt algorithm (Press *et al.* 1988). I determined the total numbers of juvenile seals ashore during the winter haulout and the moult by fitting the Rothery and McCann (1987) model to these haulouts, in the same way as for adult females in the breeding season. I determined average time ashore by tagging 70 individual seals and searching daily for these seals. Mean haulout duration was determined from the time between the first and last sighting of an individual. Adult females and adult males were assumed to spend 28 days and 40 days ashore during the moult, respectively (Ling and Bryden 1981).

## 3.3 RESULTS

### 3.3.1 Counting Errors

Most of the 1992 counts were conducted by one person, and each harem was counted at least twice. A sample of 92 counts of harems varying in size from 15 to 293 seals (mean

91.7  $\pm$  85 *sd*) that compared counts made by two people counting simultaneously and independently showed no tendency for consistent positive or negative bias. The average percentage difference on each count was  $\pm$  1.16% (range 0 - 5.5%). Repeated counts ( $n = 10$ ) of aerial photographs of harems from Doppler Hill to Spit Camp were on average 11.8% (range 9 - 13%) less than ground counts of those harems conducted on the same day as the aerial photography.

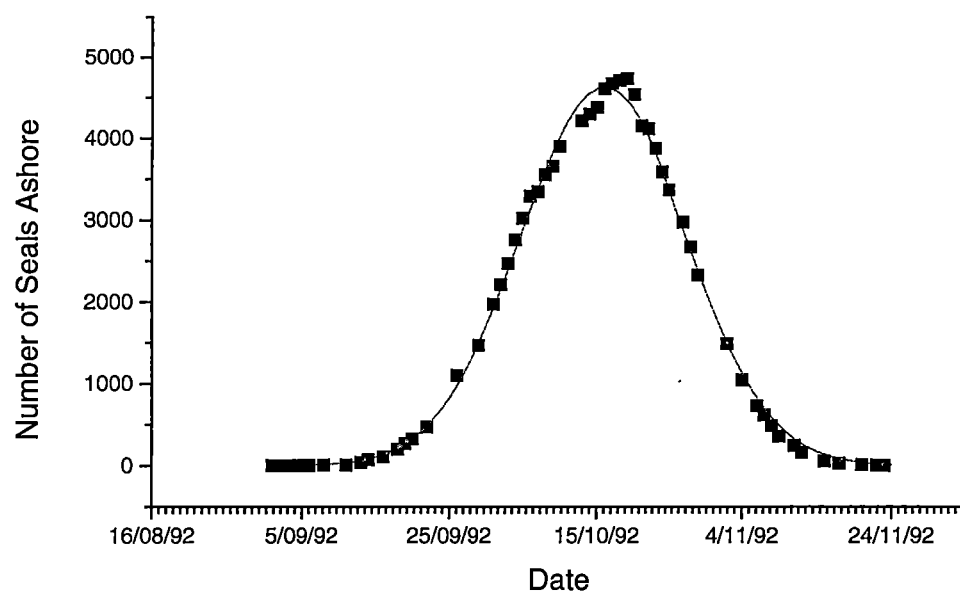
### 3.3.2 Haulout time

A total of 223 pups were weighed at birth and of these 198 were weighed at weaning. Mean duration of lactation was 21.5 days (*sd* = 1.02 days,  $n = 92$ ) for mothers with male pups and 21.5 days (*sd* = 1.00 days,  $n = 106$ ) for mothers with female pups. The mean time adult females spent ashore before parturition was 4.52 days (*sd* = 2.15 days,  $n = 80$ ). Thus, adult females were assumed to haul out, on average, for a total of 26 days during the breeding season.

### 3.3.3 Model fitting

Both the normal distribution model and the Rothery and McCann (1987) model provided good fits to the observed haulout patterns for adult females during the breeding season (Fig. 3.2). The normal distribution model and the Rothery and McCann (1987) model estimated total population size with a coefficient of variation of 0.048 and 0.036 respectively.

The Rothery and McCann (1987) model underestimated total pup production by about 4% compared to actual counts of adult females, dead pups and weaned pups in 1987 and 1992, but gave estimates of the whole population that were within  $\pm$  2.5% of the normal distribution method for all years except 1950 when the count was undertaken late in the season.



**Fig. 3.2:** Number of adult female elephant seals ashore at Spit Bay from September 1 to December 1, 1992. The curve represents a fitted normal distribution, with mean haulout .



### 3.3.4 Estimates of total breeding population

#### 3.3.4.1 1992 status

The date of maximum haulout in 1992 for breeding female elephant seals was October 16. Serial counts of harems within the prescribed study area show a normal distribution with the maximum number of cows ashore 4739 (Fig. 3.2). In the area between Compton Lagoon and Long Beach there were 14277 female elephant seals counted on the 14th, 18th, and 20th October. When this was corrected for the dates that the counts were made at each location, and an estimate of 1200 cows included for Atlas Cove, Red Island, and Saddle Point (which were inaccessible in 1992) based on the proportion of the population that was counted in those areas in 1987, the maximum number of cows ashore was 15495 (Table 3.1). The total number of dead pups in the count area in 1992 was 134 or 2.5% of total pup production.

The sum of serial counts of cows, weaned pups and dead pups reached a maximum of 5341. Thus, 88.7% of breeding adult females were present at the peak of haulout in 1992. In 1987 this figure was 87.5% at Atlas Cove. Thus, a figure of 88% was used to determine total pup production from the normal distribution model for years prior to 1987.

The normal distribution model and the Rothery and McCann (1987) model give estimates of total pup production of 17463, and 17927 respectively for Heard Island in 1992 (Table 3.2). The sex ratio at birth at Heard Island in 1992 was not different from 1:1 ( $\chi^2 = 2.80$ ,  $v = 1$ ,  $n = 223$ ,  $0.10 < p < 0.25$ ), and from life tables it can be estimated that the total population of seals of both sexes aged one year and older is 3.5 times the annual pup production (McCann 1985). Thus, in 1992 the population of elephant seals aged one year or over at Heard Island was about between 61120 and 62744.

#### 3.3.4.2 Status 1949-1987

For the 7 years where serial counts were made between 1949 and 1992, the date of maximum haulout varied from 15<sup>th</sup> to 18<sup>th</sup> October, and the standard deviation which is an

**Table 3.1:** Date of maximum haulout, standard deviation of haulout (days), maximum number of adult female elephant seals ashore at Atlas Cove and for the whole of Heard Island, and the number of serial counts (*N*) at Atlas Cove (1949-1987) or \* Spit Bay (1992).

Year	Maximum Number of Cows Ashore				
	Date	<i>sd</i>	Atlas Cove/ Spit Bay	Heard Island	<i>N</i>
1949	October 17	12.5	1798	27274	5
1950	October 18	11.5	1764	24891	6
1951	October 18	11.5	1664	25100	9
1952	October 17	11.9	1444		41
1985	October 15	11.6	1006	14456	42
1987	October 17	11.7	941	14678	55
1992	October 16	11.3	4632*	15495	56

**Table 3.2:** Elephant seal total pup production at Heard Island for Atlas Cove (1949-1987), Spit Bay (1992) and the whole island calculated from two different models. Whole island counts are presented  $\pm$  95% confidence limits.

Year	1949	1950	1951	1952	1985	1987	1992
<b>Normal Distribution Model</b>							
Atlas Cove/Spit Bay	2027	1988	1875	1627	1134	1060*	5341*
Heard Island	30739 $\pm$ 1040	28053 $\pm$ 949	28288 $\pm$ 957		16292 $\pm$ 551	16542 $\pm$ 559	17463 $\pm$ 591
<b>Rothery and McCann Model</b>							
Atlas Cove	2048	1954	1858	1612	1149	1035	5011
Heard Island	31169 $\pm$ 791	23147 $\pm$ 587	27540 $\pm$ 699		16388 $\pm$ 416	16504 $\pm$ 419	17927 $\pm$ 455

\* calculated as the maximum of the sum of adult females, dead pups, and weaned pups

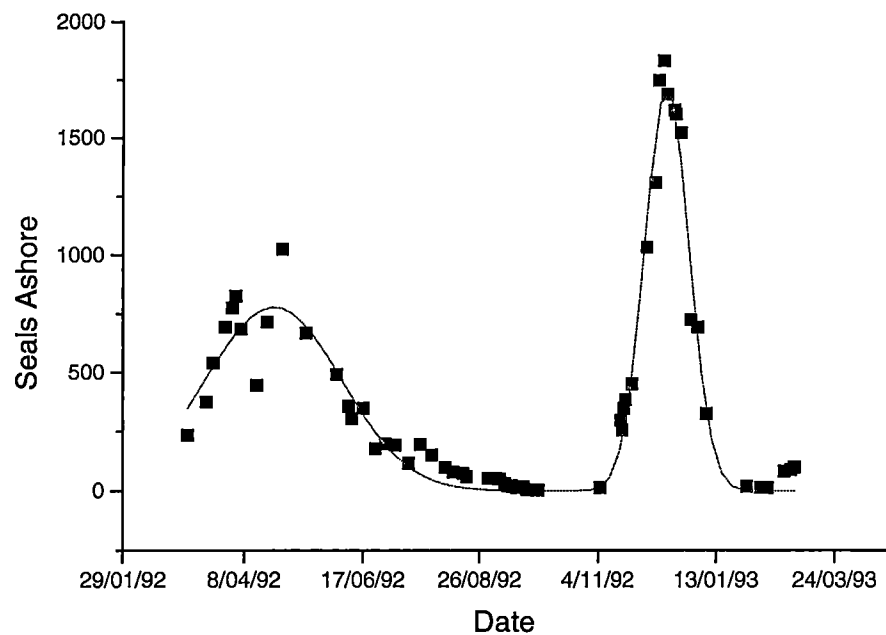
index of the length of the breeding season varied from 11.3 to 12.5 (Table 3.1). The whole island counts for 1985 and 1987 were carried out with the same methods as in 1992, although Spit Island was counted by aerial photography.

Pup production in 1949 was around 31000, and there was a slight decline in numbers over the next 3 years which is reflected in the numbers at Atlas Cove (Table 3.2). Using the 95% confidence limits on the whole island counts the population declined at between 0.5 and 4.9% per annum between 1949 and 1951. Estimates of pup production in 1985 were 44% lower at Atlas Cove and 51% lower for the whole island than in 1949. From 1949 to 1985 the population declined at between 1.6 and 1.9% per annum. Since 1985 this decline appears to have stopped (Table 3.2), with an intrinsic rate of increase of between 0 and 1.9% per annum.

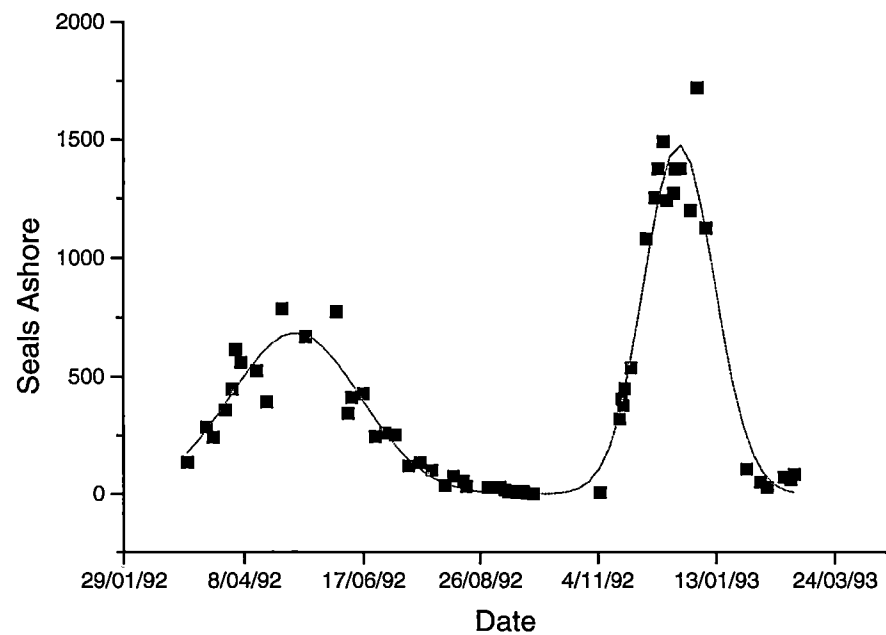
### **3.3.5 Seasonal Haulout Patterns**

#### **3.3.5.1 Juveniles**

Juvenile seals (animals in their first, second and third years of both sexes plus males less than seven years) were ashore for a longer proportion of the year than any other part of the population. They came ashore in early March and there were juveniles present throughout the winter until the breeding season. The haulouts for first year and second and third year animals followed the normal distribution (Figs. 3.3 and 3.4), and the peak of numbers of first year animals ashore was about 2 weeks earlier for second and third year animals. The longer duration of these haulouts are reflected by the much larger standard deviations of 39.38 and 38.36 days compared to the moult haulouts of 13.01 and 20.93 days for yearlings and 2-3 year olds respectively (Table 3.3). Both yearlings and 2-3 year olds returned to moult in November and the haulouts also followed the normal distribution with the maximum number of yearlings ashore occurring about a week earlier than the maximum number of 2-3 year olds (Table 3.3). Sub-adult males began hauling out in April, numbers peaked in June, and most animals had returned to sea by late August, although some animals were present during the first half of the breeding season then the sub-adult male moult



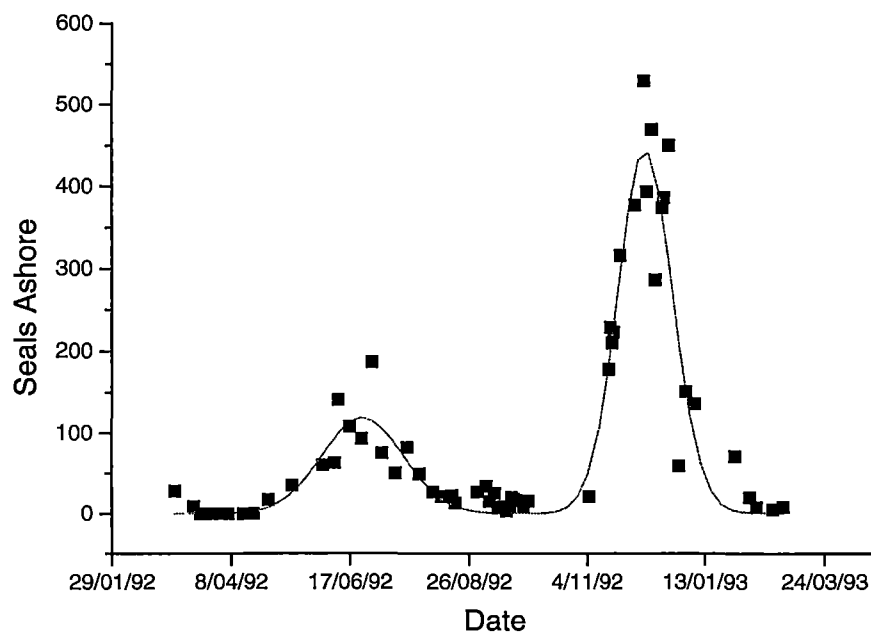
**Fig. 3.3:** Number of yearling southern elephant seals hauled out over a 12 month period at Spit Bay, Heard Island.



**Fig. 3.4:** Number of two and three year old southern elephant seals hauled out over a 12 months at Spit Bay, Heard Island.

**Table 3.3:** The date of maximum haulout and standard deviation of haulout (derived from the normal distribution function) for each of the population components of elephant seals at Heard Island, the observed and predicted maximum numbers of seals ashore and the % difference between these figures for 1992/93.

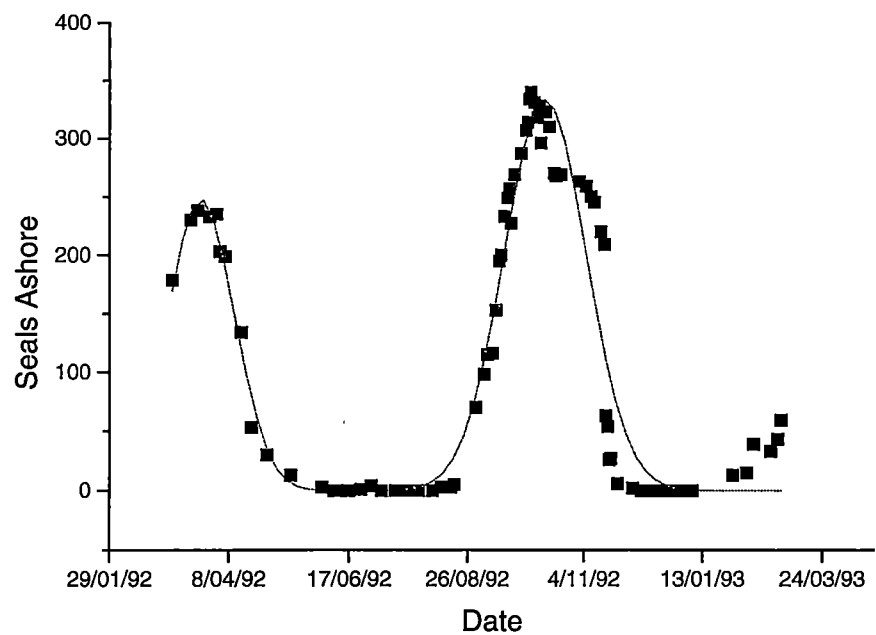
Component	Maximum Number of Seals Ashore				
	Date	sd	Observed	Predicted	% Difference
Winter Yearlings	April 25	39.38	1025	780	31.4
Winter 2-3 year olds	May 07	38.36	786	686	14.5
Winter sub-adults	June 24	23.97	187	119	37
Breeding males	October 11	24.57	340	334	1.8
Breeding females	October 16	11.31	4739	4632	2.3
Yearling Moults	December 14	13.01	1834	1723	6.4
2-3 year old moults	December 22	20.93	1490	1475	1.0
Sub-adult moults	December 08	16.41	492	445	10.5
Female moults	January 24	14.73	1143	1346	15.1
Male moults	March 22	19.24	238	247	3.6



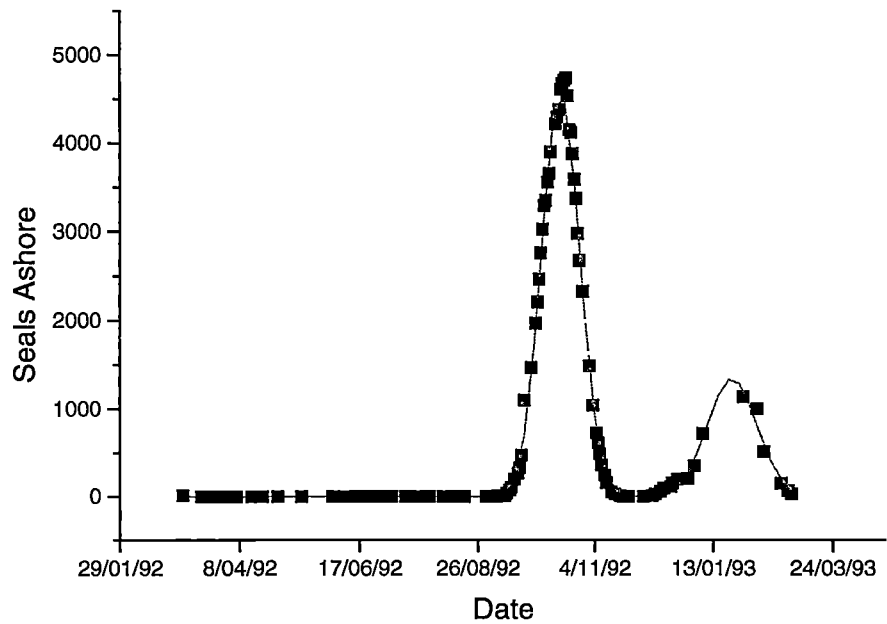
**Fig. 3.5:** Number of sub-adult male southern elephant seals hauled out over a 12 month period at Spit Bay, Heard Island.

haulout began in November and peaked in December (Fig. 3.5). The winter haulout was longer than the moult haulout as indicated by a standard deviation of 23.97 days for the sub-adult winter haulout compared to 16.41 days for the moult haulout. The normal distribution model did not predict the maximum numbers ashore during the winter haulout particularly well with the observed values being 31.4, 14.5 and 37% higher than the predicted values for yearlings, 2-3 year olds and sub-adults respectively. The observed values during the moult haulout were 6.4, 1.0, and 10.5% higher than the predicted values for yearlings, 2-3 year olds and sub adults respectively (Table 3.3).

The mean winter haulout duration for juvenile animals was  $7.01 \pm 3.2$  (*sd*) days. Using this as *S* and a peak haulout on April 25, the estimate of total number of first year animals was 11513 by the Rothery and McCann (1987) model. The serial counts represented about 95% of juveniles in the Spit Bay area. If we assume that the proportion of first year animals outside of the Spit Bay area was the same as during the breeding season then the sampling area represented about 90% of the Heard Island population, and the population of first year animals was 12792 midway through their first year. At the moult haulout the mean time ashore for yearlings was  $20.1 \pm 2.4$  days, the peak haulout was December 14, and the estimated total number of yearlings in the sampling area was 3,909. The peak moult haulout for two and three year olds was December 22, and the estimated total number of these animals in the counting area was 5726. Counts of all moulting seals at Spit Bay suggested that the sampling area represented about 40% of all moulting seals at the eastern end of the island, which gives a whole island estimate of first year animals of 10728. There are no counts of seals for 1991, so assuming pup production was about the same as in 1992 (17500), and that any movement of seals among other islands resulted in no net change in numbers, then first year survival rate was estimated at 0.613. Similarly, the moult haulout represented 5726 2-3 year olds, for an eastern Heard population of 14316 and a total island population of 15907.



**Fig. 3.6:** Number of adult male southern elephant seals hauled out over a 12 month period at Spit Bay, Heard Island.



**Fig. 3.7:** Number of adult female southern elephant seals hauled out over a 12 month period at Spit Bay, Heard Island.

### 3.3.5.2 Adults

Adult males began to haul out for the moult in late February, numbers peaked at the end of March, and all adult males had returned to sea by the end of April. Adult males began to haul out for the breeding season in the last week of August, numbers peaked on October 11, and most animals had left by the end of November (Fig. 3.6). The breeding haulout ( $sd = 24.57$ ) was longer than the moult haulout ( $sd = 19.24$ ), and the observed maximum numbers ashore were 1.8% higher in the breeding season, and 3.6% higher in the moult than the values predicted by the model (Table 3.3). The total number of adult males ashore in the area that was regularly counted during the moult was about 400, and the sampled area represented about 50% of the adult male moult population at the eastern end of Heard Island.

Adult females hauled out to moult from late December to mid March, and numbers peaked on January 24. They returned for the breeding season in the first week of September with a peak at October 16, and most had left by the last week of November (Fig. 3.7). The moult haulout ( $sd = 14.73$ ) was longer than the breeding haulout ( $sd = 11.31$ ). The observed maximum numbers ashore were 2.3% higher than the values predicted by the model for the breeding haulout, and 15.1% higher than predicted for the moult (Table 3.3). The total number of adult females ashore in the area that was regularly counted during the moult was about 1800, and the sampled area represented about 50% of the adult male moult population at the eastern end of Heard Island.

## 3.4 DISCUSSION

### 3.4.1 Possible Errors

The quality of the counts from previous years is difficult to assess although cross calibration of counters in 1992 suggested that error due to individual counters is about 1-2%. However, there were different problems associated with the counts for each year. The 1949 count included all areas of the island but it was carried out in late October, increasing the likelihood of error in the estimate of total population. For example, counts from late October



1992 gave estimates of the Spit Bay population which were 3.5% higher using the normal distribution model and 8% lower using the Rothery and McCann (1987) model. Similarly, the 1950 count was conducted in November, and counts in 1992 at the same time gave estimates for Spit Bay which were 10% lower using the normal distribution model and 16.5% lower using the Rothery and McCann (1987) model. The 1951 count was conducted in late November and early December and was a count of pups rather than adult females, and may have larger error due to the variability in the length of time pups remain on the beach after weaning and the added difficulty in counting weaners over adults. However, although the reliability of the counts over the whole island vary, the Atlas Cove counts were consistent among years, and the trend at Atlas Cove between 1949 and 1951 approximately reflects the trend for the whole island. However, if the above corrections are applied to the total population estimates for 1950 given in Table 3.2, and assuming a 5% correction for the Rothery and McCann (1987) model, then the estimates for 1950 become 30800 for the normal distribution model and 28700 for the Rothery and McCann (1987) model. This suggests that the population may have been relatively stable, or slightly declining from 1949 to 1951.

In 1985 and 1987 Spit Island was counted only by aerial photography, and ground counts and simultaneous aerial counts suggest aerial counts underestimated by about 12%. In 1992 total pup production for Atlas Cove, Saddle Point and Red Island was estimated at 1200 animals. Given the similarities of the counts for these areas in 1985 and 1987, and that for all previous whole island counts these areas accounted for between 7 and 8% of total pup production, then this estimate is probably realistic.

Both models have inherent assumptions about the biology of the animals. The slight differences in population estimates between the two models may be due to the relative strengths of these assumptions. The normal distribution model assumes that the haulout is synchronous over the whole island. This is not the case at Macquarie Island where haulout

on the eastern coast occurs later than the western coast (Slip unpublished data). The Rothery and McCann (1987) model assumes that all animals remain ashore for the same amount of time  $S$ , and this assumption also may not hold. At Macquarie Island cows early in the season tend to stay slightly longer than animals later in the season (Australian Antarctic Division, unpublished data), and at Marion Island cows which arrive early in the season tend to stay longer than those arriving late in the season (Wilkinson 1992). In addition, the Rothery and McCann (1987) model is highly sensitive to the values of the mean and standard deviation of the haulout and the haulout time (Boyd *et al.* 1996). For example, simply changing the date of mean haulout by one day produced a difference in the population estimate by about 4%. However, the serial counts on which the calculation of the mean haulout date and standard deviation of the haulout were based, were made in each year with a good spread of counts around the peak such that these variables could be determined accurately, at least for the counting area. To reduce the error due to variation in haulout behaviour at different locations around the island the serial counts in 1992 were based on about 30% of the population. In previous years serial counts were made on only about 6% of the population, increasing the possible error due to variation in haulout patterns. The estimate for time hauled out ( $S$ ), based on a lactation duration of 21.5 days, agrees with other estimates of lactation duration for animals in the Kerguelen stock as mean duration of lactation for Marion Island (Wilkinson 1992), Îles Crozet and Îles Kerguelen (Guinet 1991) all fall between 21 and 22 days.

The detailed counts of cows, dead pups and weaned pups at Spit Bay in 1992 and at Atlas Cove in 1987 suggest that the model of Rothery and McCann (1987) slightly underestimated the total population by between 1 and 2.5%. They also found at South Georgia that despite the low coefficient of variation in the model, detailed counts suggested that the model may have underestimated by up to 5%. Weaknesses in the assumptions may be the reason for the differences between the two models.

### 3.4.2 Haulout Patterns

The breeding and moult haulouts of adult seals fitted the normal distribution model well. Adult females appeared to be more synchronous with their haulouts than were adult males which may be because almost all adult females hauled out in the breeding season whereas some adult males were probably either too small or in too poor condition to be able to compete for females. The width of the moult haulouts, which is an indication of the length of time the age class is ashore but not necessarily an indication of the length of time individual seals of that age class are ashore, for yearlings sub adult males and adult females was similar, but the moult haulouts of adult males and 2-3 year olds were broader. The moult haulouts of adult males were probably broader due to animals spending longer time ashore moulting. Adult males moult for about 40 days while adult females moult for about 28 days (Ling and Bryden 1981). The broad moult haulout of 2-3 year olds may be due to this being a composite age class. These animals are very difficult to separate by eye and it may be that 3 year olds are moulting slightly later and for slightly longer than 2 year olds. Carrick *et al.* (1962) found that at Macquarie Island the moult haulouts and the winter haulouts of juvenile animals occurred later with age. This shift in the mean haulout with age may be a strategy to maximise the time spent at sea feeding during the crucial years of growth. As animals reach maturity and begin to breed their capacity to spend longer periods at sea are constrained by the synchronous haulout of breeding adults.

If the moulting peaks are consistent from year to year it may be possible to make inter-yearly comparisons of numbers of moulting seals with a series of counts on either side of the peak. However, Hindell and Burton (1988b) reported inter-annual variation in the peak of moult haulout at Macquarie Island of two weeks for adult females, and up to four weeks for adult males, although the peak for juveniles appeared to have changed little in 35 years. Also, animals tend to moult in areas of vegetation where counting is more difficult and counting errors may occur. The number of adult males ashore during the moult was much less than during the breeding season but a proportion of this population is known to moult at

ice free areas in Antarctica (Burton 1985, Gales and Burton 1989), and 29 adult males that had been tagged during the moult in Antarctica were resighted at Heard Island in 1992 (Slip 1993).

Because Heard Island is remote and rarely visited during the elephant seal breeding season it would be useful if other haulouts could be used to give at least an index of population trends. However, the Rothery and McCann (1987) model is sensitive to changes in the parameters of the model, and problems of determining time ashore accurately during the moult may make it difficult to use these haulouts for monitoring the population. The winter and moult haulouts of all age classes may be too sensitive to weather conditions to be useful for anything but broad indices of population size. Numbers of animals hauled out during the moult are known to vary on a day to day basis due to weather with both extremes of wind (cold) and sunshine (heat) resulting in seals returning to the sea (Burton 1985).

Counts of adult females during the breeding season appear to be the only reliable way of determining annual pup production and monitoring changes in the population. Both the size of Heard Island and the accessibility of hauled out seals make it relatively easy to monitor the elephant seal population there. Given the apparent stability of the population from 1985-1992, and the likelihood of increased fishing activity in the Heard Island region, it is crucial to monitor the population annually in conjunction with the development of this fishery.

### **3.4.3 Population Status**

The population of breeding females at Heard Island in 1992 appears to have changed little since 1985, and now stands at between 17000 and 18000 (Table 3.2). This represents about 30% of the entire population of the Kerguelen stock and about 9% of the world population of southern elephant seals (Laws 1994).

The models used in the present study for calculating pup production were based on recent knowledge of the biology of elephant seals, and produced slightly higher estimates of pup production than have been previously reported. For example, based on the counts from 1949 to 1952 Carrick and Ingham (1962b) estimated the Heard Island population at 23000 breeding cows, although Burton (1986) suggested that this figure should have been about 32000 based on a fixed mean haulout date of 15<sup>th</sup> October, and assuming that the maximum number of cows ashore was equal to 95% of total pup production based on data from Macquarie Island (Hindell and Burton 1988b). However, the date of maximum haulout in 1949 was 17<sup>th</sup> October and my data suggest that about 88% of the total population of adult females were ashore at the time of peak haulout which is consistent with populations at Îles Kerguelen and Îles Crozet (Guinet *et al.* 1992). Using these data in the population models my estimate of total pup production in 1949 of about 31000 is about 35% higher than the 23000 estimated by Carrick and Ingham (1962b). Pup production in 1985 was initially reported at about 13000 (Burton 1986) which again assumed that 95% of cows were ashore at peak haulout. By using a revised model, reducing assumed pup mortality to the level observed in 1992, and including a ground truthing correction for aerial counts of Spit Island my estimate of total pup production for 1985 was about 25% higher. Thus, while the population at Heard Island appears to have been relatively stable from 1985 to 1992, there is no doubt that the population has declined dramatically since 1949. The recalculated figures for total pup production in 1985 of 16300 represent only 53% of the 31000 recalculated for 1949 meaning a decline of about 47% between 1949 and 1985.

#### **3.4.4 Status at Other Localities**

The magnitude and timing of the decline at Heard Island is consistent with other Indian Ocean populations and with the population at Macquarie Island. Between 1952 and 1979 the population at Îles Kerguelen fell on two occasions, the first between 1956 and 1960, and again between 1970 and 1977, although there are no data for the period 1960 to 1970 (Pascal 1985). However, from 1984 to 1989 the population there was stable, with an overall

decrease from 1956 to 1989 of 44% (Guinet *et al.* 1992). This is remarkably similar to the situation at Heard Island where the population has been stable since 1985 with an overall decrease from 1949 to 1992 of 43%. The other Indian Ocean populations have declined but are continuing to do so. At Îles Crozet the population declined at an annual rate of 5.75% between 1966 and 1976 (Barrat and Mougín 1978), and continued to decline at 5.70% per year from 1980 to 1989 with an overall decrease in the population of 70% from 1966 to 1989 (Guinet *et al.* 1992). The Marion Island population showed a similar decrease of 69.5% from 1951 to 1986 (Wilkinson and Bester 1988). The population declined at a rate of 4.8% per annum between 1974 and 1989 but had slowed to 1.9% per annum between 1983 and 1989 (Bester and Wilkinson 1994). Between 1959 and 1985 the population at Macquarie Island declined at an average rate of 2.1% per year with an overall decrease of about 45-55% (Hindell and Burton 1987). Since 1985 the population has continued to decline but at about 1.2% per year (Antarctic Division, unpublished data). However, the population at South Georgia which constitutes 60% of the world population of southern elephant seals (Laws 1994), has not undergone the same decline but has remained relatively stable from 1952 to 1995 (Boyd *et al.* 1996), and the population at Peninsula Valdes increased over the period of 1969-1990 (Campagna and Lewis 1992).

The similarity in the population trends between Heard Island and Îles Kerguelen suggests that seals from these islands may forage in similar areas. This is further supported by seals tagged on each island being resighted at the other and in the Vestfold Hills, and animals tagged in the Vestfold Hills and the Windmill Islands being resighted at both islands (Bester 1988b, Guinet *et al.* 1992, Slip 1993). Hence, both populations may be influenced by the same changes to the marine environment. However, seals from Heard Island foraged over a large area of the Southern Ocean (this volume, Chapter 5) suggesting that any changes in the marine environment that influenced population trends must have been widespread.

The ratio of females to males ashore at the peak of the breeding season was 14:1 (Table 3.3) which is similar to the ratio at Îles Kerguelen where this ratio changed little from 1952 to 1989 suggesting that the changes in numbers of males and females have followed the same trend there (Guinet *et al.* 1992). Although there are no counts for males from the 1950's at Heard Island it seems likely that the numbers of males and females at Heard Island have followed the same trends.

### 3.4.5 Possible Causes of Population Trends

The decline in virtually all elephant seal populations of the Kerguelen and Macquarie stock groups seems to have occurred between the mid 1950's and the mid 1970's (Pascal 1985, Hindell and Burton 1987). Unfortunately, there are insufficient estimates of the populations over those years to make close comparisons of the timing of the decline. For example, there are only two estimates of the Macquarie Island population, 1959 and 1985, although there were almost annual counts of a subset of the Macquarie Island population from 1949 to the present day (Hindell and Burton 1987, Antarctic Division, unpublished data), and six estimates of the population at Îles Kerguelen 1956-1979 (Pascal 1985). However, the approximately similar timing, and magnitude of the decline in Indian Ocean and Pacific Ocean populations suggest a common cause, while differences in present day trends among different populations suggest that different factors may be operating on the populations today.

There are two age groups within the population that have been known to suffer relatively high mortality. At Macquarie Island first year survivorship appears to have been a major factor in the decline from 1959 to 1985 with survivorship reduced to almost zero in the mid 1960's (Hindell *et al.* 1994a), while at Marion Island animals in their third and fourth years appear to be the most vulnerable part of the population with some factor operating at sea causing the elevated mortality rates (Bester and Wilkinson 1994). These differences could either be interisland differences or it could be that the decline from the 1950's was

driven by different factors than those affecting the populations today. Recent data from Macquarie Island suggest that first year survivorship since 1993 has been similar to first year survivorship at Marion Island and at South Georgia (McCann 1985, Bester and Wilkinson 1994, Australian Antarctic Division, unpublished data). In addition, the estimate of first year survivorship for Heard Island given above, which was based on an estimate of first year animals hauling out to moult, gave a similar figure despite the inherent assumptions in the calculation. Whether the decline of the Kerguelen stock populations from the 1950's was also caused by massive increases in first year mortality is unknown and likely to remain so.

Several explanations have been proposed to explain the decline in the Indian and Pacific Ocean populations of southern elephant seals and these are reviewed in Hindell *et al.* (1994a). One explanation is the “overshoot” hypothesis (Hindell 1991) which proposes that commercial sealing reduced the numbers of elephant seals to such a level that their prey became abundant. Once sealing ended the seals had an abundant resource and numbers increased rapidly to “overshoot” the original population size, and the observed decline is a result of the population overexploiting its food resources and declining towards an equilibrium. Hindell (1991) proposed this as an explanation for the decline of the Macquarie Island and the Kerguelen populations. However, this hypothesis assumes there to be a simple predator-prey relationship and if the prey of the southern elephant seal were also exploited by other non-harvested predators then it is unlikely that the prey could increase in numbers (Hindell 1991). The diet of the southern elephant seal at Heard Island consists of squid and fish and most of its prey species, of similar size, were also consumed by the southern bottlenose whale (*Hyperoodon planifrons*), making this and other beaked whales potential competitors of the elephant seal (Slip *et al.* 1995, Slip 1995). An estimated 224000 - 377000 beaked whales summer in the Southern Ocean (Sekiguchi *et al.* 1993), and their potential effect on food resources make the overshoot hypothesis seem unlikely. Further, sealing occurred at different times among populations. For example, sealing occurred at Macquarie Island from 1810 to 1829 and from 1875 to 1919, with little activity between 1830 and 1974



(Hindell and Burton 1988a), while at Heard Island sealing only occurred between 1855 and 1880 (Downes 1996), and at Îles Kerguelen sealing was carried out intensively from 1840 to 1880 (Busch 1985). Sealing also occurred at Îles Kerguelen under licence between 1958 and 1962 corresponding to the initial decline (Pascal 1985).

Several authors have suggested that depletion of marine resources by commercial fisheries may have been responsible for the decline of Indian Ocean elephant seal populations (van Aarde 1980, Pascal 1985, Wilkinson and Bester 1988). The main stocks of fish on the Kerguelen shelf have been reduced by the heavy fishing effort (Duhamel and Hureau 1990), and decline at Kerguelen between 1970 and 1980 corresponds to the period of heavy unregulated fishing there. However, fish stocks have also declined at South Georgia (Kock *et al.* 1985) without a noticeable effect on the elephant seal population, and the Macquarie Island elephant seal population declined in the 1950's and 1960's with no fishing occurring in the region.

Another possible explanation is that the decline is due to changes in the ocean environment that has had an impact on the food of the southern elephant seal (Burton 1986, McCann and Rothery 1988, Hindell *et al.* 1994a). Southern elephant seals forage widely throughout the Southern Ocean and animals from the main stock groups may use the same foraging areas to some extent. For example, the recorded eastern limit of the range of the South Georgia stock overlapped with the recorded western limit of the range of the Kerguelen stock, and the recorded eastern limit of the range of the Kerguelen stock overlapped with the recorded western limit of the range of the Macquarie stock (cf. Slip *et al.* 1994, McConnell and Fedak 1996, this volume, Chapter 5). Thus, any profound environmental change to broad areas of the Southern Ocean might affect all populations of southern elephant seals.

Changes in climate in the region of the Kerguelen Plateau, and at Macquarie Island have been reported (Jacka *et al.* 1984, Allison and Keage 1986). Recently, de la Mare (1997)

reported evidence of a decline in Antarctic sea ice that occurred relatively quickly beginning in the mid 1950's and finishing by 1973. This decline was of about 2.8° of latitude averaged over October to April, and suggest a reduction of about 25% of sea ice (de la Mare 1997). The marginal sea-ice edge is an area of enhanced biological productivity (Smith and Nelson 1985). Prior to the mid 1950's and since 1973 the sea-ice has remained stable, but the decrease in sea-ice suggests that a decline in productivity of the Southern Ocean ecosystem may have occurred because the marginal sea-ice zone plays an important role in primary production (de la Mare 1997). The time scale of this environmental change correlates with observations of fluctuations in elephant seal numbers. Unfortunately, there are gaps in both the sea-ice data and particularly in the elephant seal data for most of the period 1960-1970, that make it difficult to correlate the changes. However, the sea-ice appears to have been roughly stable then decreased by about 25% over approximately the decade of the 1960's, then returned to a stable system (de la Mare 1997), while elephant seal numbers at Heard Island and Îles Kerguelen have followed a similar pattern.

If the decline in sea-ice and reduced ocean productivity was the cause of the decline in Indian Ocean and Pacific Ocean elephant seal populations why have other predators not shown similar patterns of decline? Antarctic and sub-Antarctic fur seals have been increasing since the 1980's at many sites, as have macaroni/royal and king penguins (see Hindell and Burton 1987 for references). These species were heavily exploited and in most cases the populations were just beginning to re-establish in the 1950's.

The timing of the decline in the populations at Îles Crozet, Marion Island, and Macquarie Island also corresponds to the timing of the decline in sea ice, but these populations are still declining, although in the case of Macquarie Island, at a reduced rate. One factor common to all three populations is the presence of killer whales, and predation by killer whales has been suggested as possibly a major factor in the decline of the southern elephant seal populations at Marion Island and at Îles Crozet (Condy *et al.* 1978, Guinet *et al.*

1992). At Îles Crozet observed predation by killer whales on weaned pups was 25% on one beach and actual predation was probably higher (Guinet *et al.* 1992). Killer whales were not sighted at Heard Island during 1992 (Australian Antarctic Division, unpublished data), and are rarely sighted at Îles Kerguelen (Guinet *et al.* 1992).

Given the magnitude of the declines in the Indian and Pacific Ocean populations, the similarities in behaviour at sea (Hindell *et al.* 1991a, 1991b, Slip *et al.* 1994, McConnell and Fedak 1996, this volume Chapter 5), and the overlap in foraging ranges between the populations, why has the South Georgia population remained relatively stable? The waters around South Georgia are highly productive and a proportion of the elephant seal population forage close to the island (McConnell and Fedak 1996). Boyd *et al.* (1996) suggested that while the apparent lack of change in the population of elephant seals at South Georgia may be due to unknown factors in the marine environment, it was also possible that the availability of breeding habitat may be limiting the growth of the population. If this was the case then the population at South Georgia may not be limited by food resources or other factors in the marine environment that have caused declines in the other major stocks. Alternatively, Laws (1960) suggested that sealing prior to 1952 was reducing the size of the male population, in some cases to the point of affecting recruitment, and sealing regulations were changed to address this. However, as sealing continued at South Georgia until 1964 it may be that the population had already declined prior to the first estimate of its size (Laws 1960), such that a general decline in the productivity of the ecosystem might not have affected the elephant seal population. The population at Peninsula Valdez in Patagonia has been increasing since 1969 (Campagna and Lewis 1992). It may be that the Patagonia/Falklands stock had also not recovered from exploitation by the 1960's.

Another difference among the main stocks of southern elephant seals may be the relative importance of fish in the diet. It has been difficult to assess the diet of southern elephant seals as it has not yet been possible to examine the diet at the main foraging areas.

Laws (1956) examined 139 stomachs from South Georgia 108 of which were empty, and found 26 contained squid, nine contained fish, and only six contained fresh remains, of which five contained fish and one contained squid. Thus, he suggested that elephant seals fed on fish in inshore waters and squid elsewhere (Laws 1956), and that the diet of elephant seals consisted of 75% squid and 25% fish by weight (Laws 1977). Recent studies of the diet of southern elephant seals (eg. Green and Burton 1993, Slip 1995) have noted the difficulty of quantifying the relative importance of fish and squid in the diet due to differential digestion of squid beaks and fish otoliths. However, if the relative proportion of squid and fish in the diet is calculated using the same presence/absence method used by Laws, then at Heard Island the proportions are 55% squid to 45% fish, while at Macquarie Island the proportions are 75% squid and 25% fish (Green and Burton 1993, Slip 1995). At South Georgia Rodhouse *et al.* (1992a), examined 51 stomachs from elephant seals and found squid remains in 46 but no evidence of fish remains.

This emphasis on squid at South Georgia may have insulated the population from decline in two ways: (1) the population would not be affected by commercial fisheries and (2) some of the major squid species prey on mesopelagic myctophids, which feed largely on copepods, and belong to an open-ocean food chain where krill is absent (Rodhouse and White 1995). Thus, elephant seal populations there may not be affected by the periodic fluctuations of krill resources that occur in the South Georgia region (Priddle *et al.* 1988).

### 3.5 ACKNOWLEDGEMENTS

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## CHAPTER 4

### THE DIET OF SOUTHERN ELEPHANT SEALS (*MIROUNGA LEONINA*) FROM HEARD ISLAND<sup>1</sup>

#### 4.1 INTRODUCTION

The southern elephant seal (*Mirounga leonina*) ranges throughout the Southern Ocean with its major breeding populations occurring on South Georgia, Macquarie Island, and Îles Kerguelen-Heard Island (Reeves *et al.* 1992, Laws 1994). Populations of southern elephant seals in the Indian and Pacific sectors of the Southern Ocean have decreased substantially over the past several decades (Laws 1994). At Heard Island and Macquarie Island, the populations have declined by 40 to 50% (Burton 1986, Hindell and Burton 1987). A primary factor in these declines seems to have been increased mortality of seals during their first year at sea, particularly for those born at Macquarie Island. Hindell (1991) suggested that changes in distribution and abundance of prey could be a proximate cause of reduced survival of young seals. However, the diet of juvenile elephant seals, particularly of animals in their first year, is poorly known, although it is important in evaluating the role of food in demographic change.

Although squid and fish have been known to be important components of the diet of the southern elephant seal (Laws 1956, 1960, 1977), few studies have examined the diet in detail (e.g., Rodhouse *et al.* 1992a, Green and Burton 1993). An earlier study of the diet of elephant seals at Heard Island identified 14 species of cephalopods from 11 families in the stomachs of 11 adult males, 26 adult females, 12 subadult animals, and seven juveniles in summer (Green and Burton 1993). *Moroteuthis ingens* was the most important cephalopod species by number, mass and percent occurrence in the stomachs of adult females. In addition, Green and Burton (1993) reported that 77.2% of seals sampled had eaten fish of 11

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taxa, including pelagic, benthic, and benthopelagic species. Dietary data indicate that southern elephant seals from Heard Island spend more time foraging in Antarctic waters than do seals from Macquarie Island (Green and Burton 1993). Similarly, elephant seals from South Georgia mostly forage in areas south of the Antarctic Polar Front (Rodhouse *et al.* 1992a).

No previous studies have examined the diet of southern elephant seal pups during their first year at sea. Differences in diet between adults and juveniles might be expected because of apparent differences in their distribution. For example, adult southern elephant seals haul out on subantarctic islands almost exclusively for moulting and breeding, while immature animals (including those in their first year at sea) have a winter haulout as well as a summer moult haulout at the end of the breeding season (Hindell and Burton 1988b). I studied pups and adult southern elephant seals at Heard Island in 1992-1993, to determine whether there were important differences in species composition or prey size. Here I present the results of these studies and compare them with those of prior studies from the same and other colonies.

## 4.2 MATERIALS AND METHODS

I lavaged the stomachs of southern elephant seals at Spit Bay near the eastern end of Heard Island (53° 05' S, 73° 45' E) in July and August 1992 (juveniles), and from January through March 1993 (adults). I chemically immobilised seals with a combination of ketamine and diazepam soon after they came ashore. I injected the mixture either intramuscularly via a long plastic tube (adults; see Woods *et al.* 1989), or intravenously after first restraining the animal manually with a canvas head bag (pups of the year and yearlings; see Slip and Woods, 1996). I then inserted a soft plastic tube (30 mm internal diameter for juveniles and adult females, 40 mm internal diameter for adult males) down the oesophagus and into the stomach, and pumped fresh water or seawater into the stomach with a mechanical hand pump. Depending on the size of the animal, four to 16 litres of water were

used. When enough water was pumped into the stomach, the animal began to regurgitate and the open end of the tube was dropped below the level of the stomach to aid in the removal of the stomach contents. Regurgitant was filtered through a 1-mm sieve to retrieve the stomach contents. I repeated the procedure up to four times until the material flushed was largely clear of stomach contents. I tagged each seal in its hind flippers with plastic Jumbo Rototags (Dalton Supplies, Woolgoolga, NSW, Australia), and measured standard length (STL), girth, and mass when possible, and classified juvenile seals as pups of the year if  $STL < 1.89$  m and yearlings if  $1.89 \text{ m} < STL < 2.15$  m (Arnbom *et al.* 1992, Rodhouse *et al.* 1992a). I washed the recovered items thoroughly, stored them in ethanol, and later identified them to genus or species where possible using voucher specimens and descriptions of cephalopod mouthparts in Clarke (1986). I measured lower rostral lengths (LRL) to the nearest 0.1 mm using vernier callipers, and used allometric regression equations to estimate whole wet body mass and dorsal mantle length (DML) from LRL (Clarke 1986, Rodhouse 1989a, Rodhouse *et al.* 1990). I classified the squid prey as Antarctic, (species that occur south of the Antarctic Polar Front), subantarctic (species that occur south of the subtropical convergence), and cosmopolitan (species that are widespread), following Roper *et al.* (1985), Rodhouse *et al.* (1987), and Rodhouse (1990). I identified fish otoliths from voucher specimens in the Australian Antarctic Division and by reference to descriptions by Williams and McEldowney (1990).

I used principal coordinates analysis (PCA, Belbin 1993) to (i) compare the dietary composition of male and female seals of different ages, and (ii) examine annual changes in dietary composition, using data for adult males and adult females from 1987-88 (Green and Burton 1993). Where the PCA produced discreet groups, these were tested for statistical significance using the Mantel Test, a nonparametric randomization type test that estimates the degree of resemblance between two distance-type matrices (Patterson 1986, Belbin 1993).

### 4.3 RESULTS

I retrieved prey remains from 76 elephant seals. Thirty two seals were juveniles (24 males, 8 females), 38 were adult females (6 breeding, 32 moulting), and six were moulting adult males. Twenty six of the juveniles were judged to be pups of the year ( $STL < 1.89$  m) and the other six were yearlings ( $1.89 \text{ m} < STL < 2.15 \text{ m}$ ).

Remains of prey were recovered from 72% of juvenile stomachs (all of which were pups of the year), and all of these had eaten squid. Fish remains (otoliths, bones, and eye lenses) occurred in 63% of samples, amphipods in 41%, and other crustacea in 19% of stomachs. All moulting adult females had eaten squid, 84% had eaten fish, 53% had eaten ascidians, and 39% had eaten crustaceans or other invertebrates. Six stomach samples were obtained *post-mortem* from adult females which had been killed by an adult male during the breeding season. All had eaten squid, one (17%) had eaten fish, three (50%) had eaten ascidians, and one (17%) had eaten crustaceans. All adult males had eaten squid, 50% had eaten fish, 50% had eaten euphausiids and other crustaceans, and 17% had eaten ascidians (Table 4.1).

#### 4.3.1 Species composition of cephalopod prey

Squid remains from 17 taxa were identified from 86% of stomachs of southern elephant seals. A total of 1492 lower beaks representing an estimated 445.4 kg wet mass of cephalopods were identified and measured.

The highest contribution by number was the small psychroteuthid squid *Psychroteuthis glacialis* (21.1%), and the four most common species, *P. glacialis*, *Moroteuthis knipovitchi*, *Gonatus antarcticus* and *Kondakovia longimana*, accounted for 63.2% of beaks by number, while nine species accounted for 93.9% of beaks (Table 4.2). In terms of mass, the seals' diet was dominated by the large Antarctic species *K. longimana* (40.4%). Four species, *K. longimana*, *M. knipovitchi*, *M. ingens*, and *Alluroteuthis*



**Table 4.1:** Frequency of occurrence (%) of prey in the stomachs of southern elephant seals at Heard Island in 1992-1993.

	Juveniles	Adult Males	Adult Females	All
	( <i>n</i> = 32)	( <i>n</i> = 6)	( <i>n</i> = 38)	( <i>n</i> = 76)
Fish	63	33	74	66
Squid	72	100	100	86
Crustacean	56	50	42	49
Ascidian	0	17	53	28
Stomachs with prey	72	100	100	86

**Table 4.2:** Squid taxa identified from beaks in the stomachs of southern elephant seals at Heard Island, according to age-class, sex and season, expressed as a percentage of the total number of beaks.

Age Class	Juveniles			Adults			All age Classes
Sex	Male,	Female,	All,	Male,	Female,	Female,	
Season	winter	winter	winter	summer	summer	winter	
<i>Alluroteuthis antarcticus</i>	0.7	0.0	0.5	6.5	8.9	6.9	7.1
<i>Brachioteuthis</i> sp.	0.7	0.0	0.5	0.0	4.1	1.7	2.7
<i>Chroteuthis</i> sp.	0.0	0.0	0.0	1.0	1.9	1.2	1.4
<i>Galiteuthis glacialis</i>	0.0	0.0	0.0	12.0	2.4	10.6	5.2
<i>Gonatus antarcticus</i>	33.6	12.8	29.1	15.0	9.4	16.1	14.0
<i>Histioteuthis eltaninae</i>	1.4	0.0	1.1	0.0	0.4	2.1	0.9
<i>Kondakovia longimana</i>	3.5	0.0	2.7	16.7	9.8	24.8	13.7
<i>Liocranchia</i> sp.	0.0	0.0	0.0	0.0	0.0	0.2	0.1
<i>Martialia hyadesi</i>	17.5	43.6	23.1	0.0	0.4	4.5	4.3
<i>Mastigoteuthis</i> sp. B	0.0	0.0	0.0	0.0	0.1	0.0	0.1
<i>Mastigoteuthis</i> sp.?	26.6	33.3	28.0	6.5	6.5	6.4	9.1
<i>Moroteuthis ingens</i>	0.7	0.0	0.5	0.0	8.5	1.9	5.0
<i>Moroteuthis knipovitchi</i>	7.7	0.0	6.0	10.2	19.8	9.7	14.5
<i>Psychroteuthis glacialis</i>	0.0	7.7	1.6	33.3	27.9	13.7	21.0
<i>Taonius pavo</i>	0.0	0.0	0.0	0.0	0.0	0.2	0.1
<i>Todarodes filippovae</i>	5.6	0.0	4.4	0.0	0.0	0.0	0.5
unknown A	2.1	2.6	2.2	0.0	0.0	0.0	0.3
Total number of beaks	143	39	182	108	779	423	1492

*antarcticus*, accounted for 82.7% of squid by mass, while nine species accounted for 96.5% of squid by mass (Table 4.3). Five species, *M. knipovitchi*, *G. antarcticus*, *Brachioteuthis* sp., *K. longimana*, and *A. antarcticus*, occurred in over 20% of stomachs (Table 4.4).

Species of cephalopods that were eaten and are known to occur at or south of the Antarctic Polar Front are: *P. glacialis*, *K. longimana*, *M. ingens*, *M. knipovitchi*, *G. antarcticus*, *A. antarcticus*, *Galiteuthis glacialis*, *Brachioteuthis* sp., *Chiroteuthis* sp., and *Martialia hyadesi*. *Taonius pavo* is a cosmopolitan species that also occurs south of the Antarctic Polar Front. The distributions of *Liocranchia* sp., *Mastigoteuthis* sp.?, and *Mastigoteuthis* sp. B are poorly known. Antarctic species accounted for 89% by number and 97% by mass of cephalopod prey consumed by all classes of elephant seals. However, Antarctic species are less represented in the juvenile diet, accounting for 64% by number and 71% by mass of cephalopod prey consumed by juveniles.

#### 4.3.2 Effects of sex, age and year on composition of the diet

Principle coordinates analysis performed on the presence or absence of all identifiable prey (Table 4.4) produced the groupings illustrated in Fig. 4.1. The first three vectors explained 64% of the total variance, with 91% of total variance explained by five vectors. The PCA loadings were used to interpret the position of the groups and the most important contributors are shown on the axes in Fig. 4.1. The highest loadings on vector 1 were fish remains and *Todarodes filippovae* (positive), and *A. antarcticus* and *P. glacialis* (negative), while the highest loadings on vector 3 were *Martialia hyadesi* and *Mastigoteuthis* sp.? (positive) and *Histioteuthis eltaninae* and *Moroteuthis knipovitchi* (negative).

There was substantial overlap in the diets of adult males and adult females regardless of the year when data were collected. The only group which showed separation was the juveniles. Although juveniles ate more fish than adults, they also ate proportionally more of the cephalopods *Martialia hyadesi*, *Mastigoteuthis* sp.? and *Gonatus antarcticus* than adults.

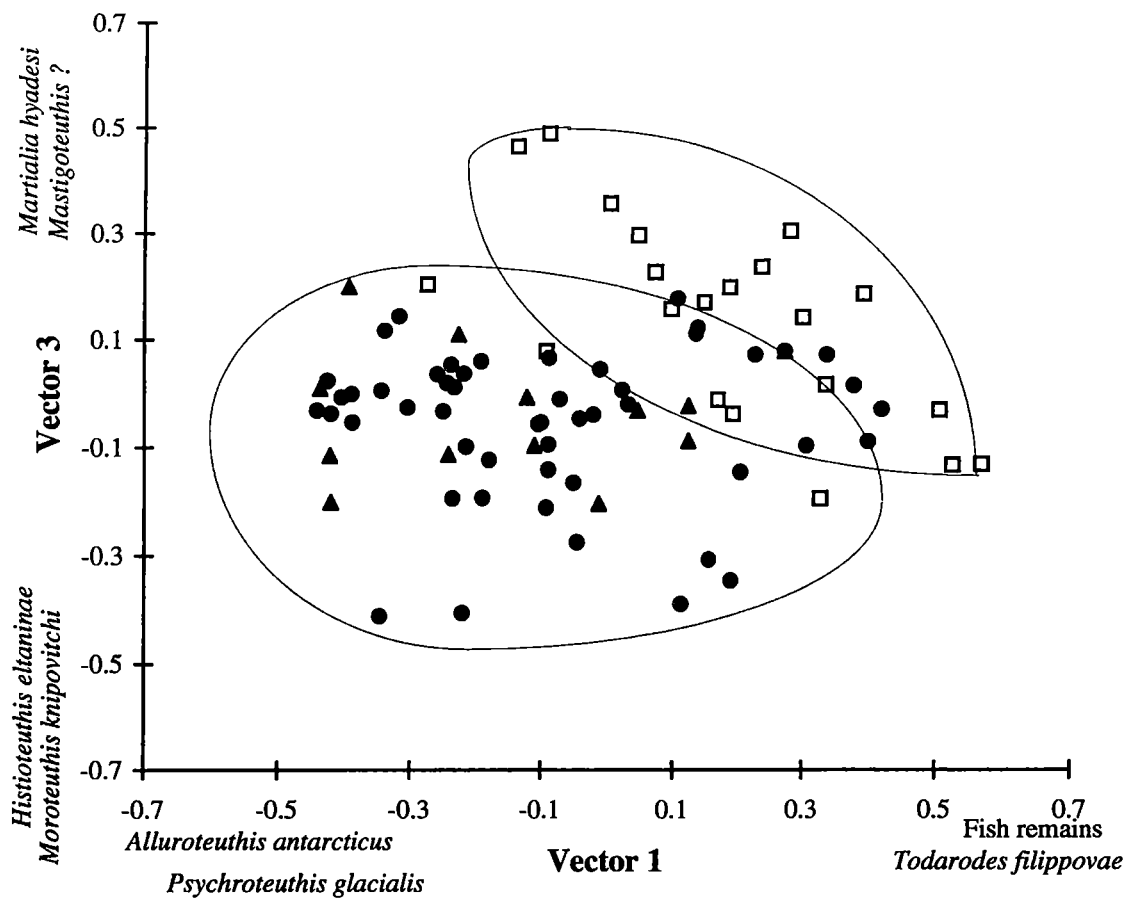
**Table 4.3:** Squid taxa identified from beaks in the stomachs of southern elephant seals at Heard Island, according to age class, sex and season, expressed as a percentage of the total calculated mass.

	Juveniles			Adults			All Age Classes
	Male, winter	Female, winter	All, winter	Male, summer	Female, summer	Female, winter	
<i>Alluroteuthis antarcticus</i>	0.9	0.0	0.7	6.8	12.6	9.5	10.2
<i>Brachioteuthis</i> sp.	0.1	0.0	0.0	0.0	0.2	0.0	0.1
<i>Chiroteuthis</i> sp.	0.0	0.0	0.0	0.02	0.2	0.1	0.1
<i>Galiteuthis glacialis</i>	0.0	0.0	0.0	1.2	0.5	1.1	0.7
<i>Gonatus antarcticus</i>	3.6	1.0	3.0	3.1	3.2	3.0	3.1
<i>Histioteuthis eltaninae</i>	0.3	0.0	0.2	0.0	0.1	0.4	0.2
<i>Kondakovia longimana</i>	3.4	0.0	2.6	71.8	25.0	68.1	40.7
<i>Liocranchia</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.01
<i>Martialia hyadesi</i>	45.5	94.4	57.1	0.0	0.2	2.1	4.8
<i>Mastigoteuthis</i> sp. B	0.0	0.0	0.0	0.0	0.0	0.0	0.01
<i>Mastigoteuthis</i> sp.?	2.0	2.9	2.2	0.4	0.5	0.4	0.6
<i>Moroteuthis ingens</i>	1.2	0.0	0.9	0.0	21.5	4.9	13.0
<i>Moroteuthis knipovitchi</i>	9.1	0.0	7.0	9.5	28.6	8.9	19.4
<i>Psychroteuthis glacialis</i>	0.0	1.7	0.4	7.1	7.5	1.3	5.2
<i>Taonius pavo</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.01
<i>Todarodes filippovae</i>	33.9	0.0	25.9	0.0	0.0	0.0	1.8
<b>Total (g)</b>	<b>24218</b>	<b>7516</b>	<b>31734</b>	<b>50938</b>	<b>239638</b>	<b>123042</b>	<b>445352</b>

**Table 4.4:** Frequency of occurrence (%) of squid taxa identified from beaks, fish taxa identified from otoliths, and other identifiable remains from stomachs of southern elephant seals at Heard Island, according to age class, sex and season.

	Juveniles			Adults			All (n = 79)
	Female,	Male,	All,	Female,	Female,	Male,	
	winter (n = 8)	winter (n = 24)	winter (n = 32)	winter (n = 6)	summer (n = 32)	summer (n = 6)	
<i>Alluroteuthis antarcticus</i>	0	4	3	67	44	50	29
<i>Brachioteuthis</i> sp.	0	4	3	67	25	0	17
<i>Chroteuthis</i> sp.	0	0	0	33	13	17	9
<i>Galiteuthis glacialis</i>	0	0	0	33	38	50	22
<i>Gonatus antarcticus</i>	50	25	34	67	56	100	51
<i>Histioteuthis eltaninae</i>	0	4	3	50	6	0	8
<i>Kondakovia longimana</i>	0	14	13	67	53	67	38
<i>Liocranchia</i> sp.	0	0	0	17	0	0	1
<i>Martialia hyadesi</i>	25	11	16	17	6	0	11
<i>Mastigoteuthis</i> sp. B	0	0	0	0	3	0	1
<i>Mastigoteuthis</i> sp.?	50	39	47	67	53	33	50
<i>Moroteuthis ingens</i>	0	4	3	33	53	0	26
<i>Moroteuthis knipovitchi</i>	0	18	16	67	66	50	43
<i>Psychroteuthis glacialis</i>	25	0	6	50	66	67	39
<i>Taonius pavo</i>	0	0	0	17	0	0	1
<i>Todarodes filippovae</i>	0	18	16	0	0	0	7
Unknown species A	13	11	13	0	0	0	5
<i>Electrona carlsbergi</i>	25	4	9	17	16	0	12
<i>Dissostichus eleginoides</i>	0	0	0	0	6	17	4
<i>Gymnoscopelus nicholsi</i>	0	0	0	0	9	0	4
<i>Electrona antarctica</i>	13	0	3	0	3	0	3
Fish eye	63	46	56	0	81	17	59
Fish bone	0	11	9	0	0	0	4
All fish remains	63	54	63	17	84	50	66
Ascidians	0	0	0	50	53	17	28
<i>Themisto gaudichaudii</i>	38	36	41	0	0	50	21
Euphausiid sp.	25	14	19	0	0	50	12
Other invertebrates	0	0	0	0	9	0	4

Note: *n* is the number of animals



**Fig. 4.1:** Two dimensional plot of vectors 1 and 3 from Principle Coordinates Analysis which demonstrates separation of dietary composition between adults males (▲), adult females (●), and juveniles (□). The first three vectors explained 64% of variance. Names along the axes indicate those components which had highest vector loadings.

The composition of the cephalopod component of the diet of adults was significantly different from that of juveniles (Mantel test  $p > 0.05$ ).

### 4.3.3 Size of Cephalopod Prey

The mean lower rostral length, mean estimated dorsal mantle length and mean estimated mass for species of cephalopods taken by juvenile, adult female and adult male elephant seals are given in Table 4.5. The relationship between the LRL of cephalopods taken and seal body length was examined for *Gonatus antarcticus*, *Kondakovia longimana*, and *Moroteuthis knipovitchi*. These were the only squid species that were eaten by more than 10 seals in each age and gender category. Asymptotic regression models were fitted for these species, and showed a trend for small seals to take smaller prey (Fig 4.2).

### 4.3.4 Fish and Invertebrates

Sixty six percent of all seals had eaten fish. Fish otoliths from four species were identifiable from stomachs of two adult males, five adult females, one juvenile male, and two juvenile females (Table 4.6). Fish species included *Electrona antarctica*, *Electrona carlsbergi*, and *Gymnoscopelus nicholsi* which are meso-pelagic, and the benthic-pelagic *Dissostichus eleginoides*. Mean standard lengths were  $440.5 \pm 116.3$  mm for *D. eleginoides* (approximate range of mass 200 - 4000 g),  $137.4 \pm 5.0$  mm for *E. antarctica* (30 - 50 g),  $77.0 \pm 10.0$  mm for *E. carlsbergi* (5 - 15 g) and  $65.5 \pm 21.5$  mm for *G. nicholsi* (5 - 15 g).

The crustacean species *Themisto gaudichaudii*, *Hyperiella* sp., *Euphausia superba* and *Euphausia vallentini* were identified from the stomachs of 37 seals (Table 4.1).

## 4.4 DISCUSSION

### 4.4.1 Dietary composition

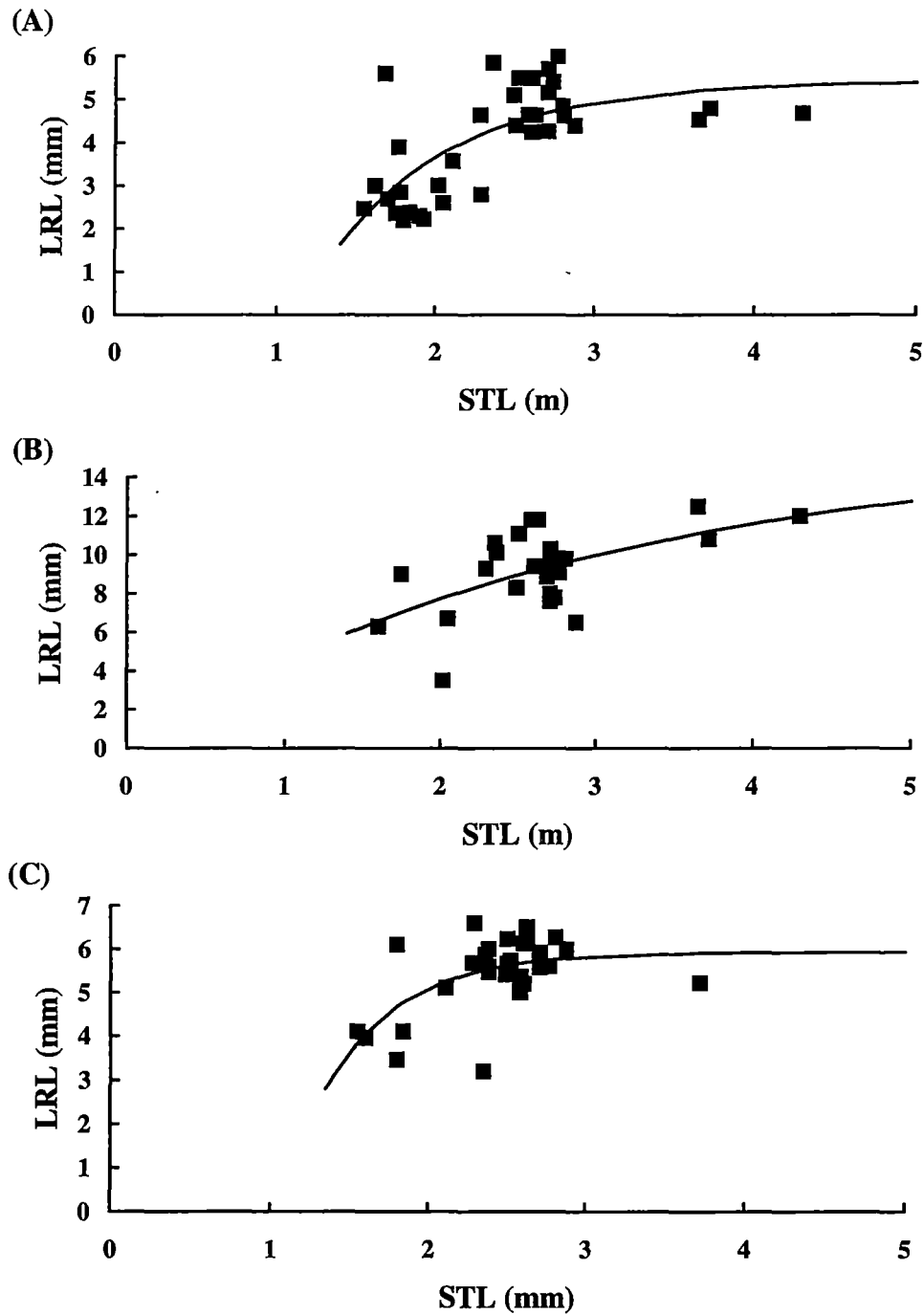
The composition of the cephalopod diet of adult males, adult females and juveniles were dominated by six species, *Psychroteuthis glacialis*, *Moroteuthis knipovitchi*, *M. ingens*, *Kondakovia longimana*, *Gonatus antarcticus*, and *Alluroteuthis antarcticus*. These species

**Table 4.5:** Lower rostral length (LRL, mm), estimated mantle length (ML, mm), and estimated mass (M, g) of squid eaten by adult male, adult female, and juvenile southern elephant seals at Heard Island.

	Juveniles								Adult males								Adult females							
	LRL		ML		M		n		LRL		ML		M		n		LRL		ML		M		n	
	Mean	sd	Mean	sd	Mean	sd			Mean	sd	Mean	sd	Mean	sd			Mean	sd	Mean	sd	Mean	sd		
<i>Alluroteuthis antarcticus</i>	4.1		125		216		1		5.4	0.4	165	12.3	496	110.6	7		5.1	0.7	155	22.5	428	148.8	98	
<i>Brachioteuthis</i> sp.	4.1						1								0		4.0	0.6	97	11.4	12	2.4	39	
<i>Chroteuthis</i> sp.							0		2.2		65.2		7		1		3.8	0.5	105	13.1	31	11.6	20	
<i>Galiteuthis glacialis</i>							0		3.7	0.8	165	33.2	48	23.7	13		3.4	0.8	150	32.6	39	22.2	64	
<i>Gonatus antarcticus</i>	2.6	0.7	69	30.1	18	28.8	53		4.9	0.5	166	23.2	107.6	37.2	12		4.3	0.9	143	37.7	80	54.1	141	
<i>Histioteuthis eltaninae</i>	2.4		40		7.2		2								0		2.8	0.3	49	6.3	55	12.6	12	
<i>Kondakovia longimana</i>	6.9	2.3	279	73.5	165	170.8	5		11.8	2.2	523	95.3	2032	2113	18		8.8	2.7	391	119.2	794	2061	181	
<i>Liocranchia</i> sp.							0								0		2.2		179		38		1	
<i>Martialia hyadesi</i>	6.0	1.5	279	43.1	31	172.1	42								0		3.4	0.7	203	20.7	137	55.1	22	
<i>Mastigoteuthis</i> sp. B							0								0		3.7		215		52		1	
<i>Mastigoteuthis</i> sp.?	2.3	0.4	64	11.6	14	7.6	51		3.1	0.3	88	9.1	32	9.4	7		2.6	0.6	73	17.3	22	24.6	78	
<i>Moroteuthis ingens</i>	5.2		179		772		1								0		6.3	1.5	295	157.7	778	1095	74	
<i>Moroteuthis knipovitchi</i>	4.3	1.2	96	108.7	201	204.5	11		5.7	0.6	237	58.7	441	144.6	11		5.5	0.9	215	85.3	408	197.6	195	
<i>Psychroteuthis glacialis</i>	3.6	0.3	123	19.5	42	15.8	3		4.3	0.4	170	25.6	100	38.5	36		3.9	0.7	142	45.1	71	40.1	275	
<i>Taonius pavo</i>							0								0		4.4		258		56		1	
<i>Todarodes filippovae</i>	7.1	1	311	311	1026	365	8								0								0	

Note: *n* is the number of individuals of the squid taxon found.





**Fig. 4.2:** The relationship between lower rostral length (LRL) of cephalopod prey and standard length (STL) of elephant seals for three species of squid. Asymptotic regressions were fitted using the model  $y = \alpha - \beta \cdot \delta^x$  for the squid species :

(a) *Gonatus antarcticus* :  $LRL = 5.438 - (22.312 * 0.282^{STL})$ , corrected  $r^2 = 0.469$

(b) *Kondakovia longimana* :  $LRL = 15.509 - (15.539 * 0.707^{STL})$ , corrected  $r^2 = 0.317$

(c) *Moroteuthis knipovitchi* :  $LRL = 5.932 - (48.676 * 0.131^{STL})$ , corrected  $r^2 = 0.348$

**Table 4.6:** Number of otoliths from which fish taxa were identified from the stomachs of southern elephant seals at Heard Island according to age-class, sex, and season.

	Juveniles		Adults		All
	Female,	Male,	Female,	Male,	
	winter	winter	summer	summer	
<i>Electrona carlsbergi</i>	6 (2)	1 (1)	49 (4)	0	59 (8)
<i>Dissostichus eleginoides</i>	0	0	3 (2)	18 (1)	21 (3)
<i>Gymnoscopelus nicholsi</i>	0	0	6 (3)	0	6 (3)
<i>Electrona antarctica</i>	2 (1)	0	6 (1)	0	8 (2)

Note: Numbers in parentheses show the number of individual stomachs from which otoliths were recovered.

accounted for 91% of the biomass represented by the beaks. Although these species are all relatively large muscular squid (Roper *et al.* 1985, Rodhouse *et al.* 1992a), seals mostly ate relatively small representatives of their respective species (Table 4.5). These species were also reported as common prey (both in terms of number and mass) of elephant seals from Heard Island in earlier studies (Green and Burton 1993), and from South Georgia, with the exception of *M. ingens* and the addition of *Martialia hyadesi* (Rodhouse *et al.* 1992a).

Others have reported octopods as prey of the southern elephant seal, although they were not eaten often (Clarke and MacLeod 1982, Rodhouse *et al.* 1992a, Green and Burton 1993). That I found no octopods in the stomachs of seals at Heard Island is most likely a consequence of the very small number of adult males that I examined, as these animals are most likely to feed benthically (Hindell *et al.* 1991b).

Although crustaceans were often recovered, their dietary significance is not clear. Most may have been ingested incidentally to normal feeding or they may have been secondary prey of squid or fish. For example, the squid *K. longimana* is known to prey on the isopod *Thermisto gaudichaudii* (Nemoto *et al.* 1985). Furthermore, the actual biomass of invertebrates consumed appears to be insignificant. Nonetheless, crustaceans have been reported as primary prey of the southern elephant seal by Green and Burton (1993).

The proportion of elephant seal stomachs that contained fish remains (66%) was slightly lower than the 77% found at Heard Island in 1987-1988 (Green and Burton 1993). In addition, fewer fish species were identified from otoliths in the present study than in 1987-88, although otoliths were found in 16 stomachs compared with three in 1987-1988 (Green and Burton 1993). The Patagonian tooth fish, *Dissostichus eleginoides*, is a newly identified prey of the southern elephant seal. It is a benthic-pelagic species common on the Kerguelen shelf and upper slope at depths of between 70 and 1500 m (Fischer and Hureau 1985). Younger fish up to 500 mm in length are mostly found in shallow water (Williams and McEldowney 1990).

Although fish remains occurred in stomachs of southern elephant seals less often than cephalopods (Table 4.1), it is difficult to quantify the relative importance of each because of differential digestion of squid beaks and fish otoliths. The diversity of fish in the diet of the seals was substantially less than that of squid. Antonelis *et al.* (1987, 1994) reported a similar pattern in northern elephant seals, *Mirounga angustirostris*. However, Stewart and DeLong (1993) suggested that mesopelagic fish may be an important prey of northern elephant seals in areas where mesopelagic fish and squid distributions are highly correlated, although lavage studies of seals ashore may not detect them. Given the similarities in diving behaviour between the two elephant seal species (cf. DeLong and Stewart 1991, Le Boeuf 1994, Slip *et al.* 1994) this may also be true for the southern elephant seal. *Moroteuthis knipovitchi* of mantle lengths 135-355 mm are known to feed on myctophid and other Antarctic fish in the mesopelagic layer (Nemoto *et al.* 1985).

A lack of information on the elephant seals' diet during most of the year when they are away from their subantarctic island rookeries remains a substantial barrier to a full understanding of their foraging ecology. Adult southern elephant seals from Heard Island migrated to the Antarctic Continental Shelf in winter (males and females), and foraged along the southeast edge of the Kerguelen Plateau in summer (females) (this volume, Chapter 5).

#### 4.4.2 Gender differences

The extreme sexual dimorphism of the southern elephant seal and the differences in foraging areas and diving behaviour between the sexes (Hindell *et al.* 1991a, 1991b, this volume, Chapter 5) suggest that sex differences in the diet may occur. However, apart from the tendency of adult males to take slightly larger specimens of some squid species, particularly the large onychoteuthid *Kondakovia longimana* (Table 4.5), no sex differences in diet composition were evident. Adult males may be better able to capture larger prey than adult females simply because of their larger and stronger mouths. In addition, adult males may take larger fish than adult females, as all but two of the otoliths from *Dissostichus*

*eleginoides* came from the stomach of a single adult male (Table 4.6) with some otoliths representing fish up to 4000 g.

The lack of any gender differences in dietary composition may merely reflect the method of sampling animals that had recently foraged in the same habitat as they returned to land and may not reflect differences that occur when the animals are over their main foraging areas. Male and female northern elephant seals eat similar prey in areas close to their haulout sites (Antonelis *et al.* 1994), but Stewart and DeLong (1994) reported that males and females foraged at different depths during their foraging migration, which led them to propose that males and females may be foraging on different size classes of prey.

#### 4.4.3 Interannual differences

Small samples from earlier years (Green and Burton 1993) limit interannual comparisons. However, the diet was quite similar among years. The main difference was the presence of *M. hyadesi* in the present study (cf. Table 4.2 and Green and Burton 1993). Other differences were minor: the presence of *Liocranchia* sp. and *Mastigoteuthis* sp B, (each occurring in one seal), and the absence of *Pholidoteuthis* sp. in 1992-93. There was a reduction in the relative importance of *M. ingens* and *M. knipovitchi* in the diet of adult females, whereas the importance of *P. glacialis* increased. As *P. glacialis* is widespread south of the Antarctic Polar Front (Rodhouse 1989a, 1990) this difference might be due to females ranging further south in 1992-1993 than in 1987-1988. Similar interannual differences were reported for southern elephant seals at South Georgia, where the composition of cephalopods were broadly similar between years but the relative importance of a few species changed (Rodhouse *et al.* 1992a). However, if seals are very faithful to particular areas or particular means for foraging, these slight seasonal differences might not reflect overall differences but simply indicate that different animals were sampled each year.

Owing to the diversity of cephalopod prey in the diet of elephant seals, interannual differences in diet composition may be minor unless large-scale physical changes in the

marine environment act differentially on some cephalopod species. How environmental fluctuations might affect the distribution and abundance of the cephalopod prey of the southern elephant seal is unclear. However, large-scale oceanic environmental changes are known to affect the distribution and abundance of krill (Priddle *et al.* 1988) and mesopelagic myctophid fish (Kozlov *et al.* 1990), and although there are few data on the prey of Southern Ocean cephalopods, it is likely that krill and myctophids are a major food source for many species, including those that southern elephant seals seek (Rodhouse 1989b, Rodhouse and White 1995). There is a marked association of the distribution of cephalopod species and large-scale oceanographic features and the mesoscale eddies and fronts in the southern Atlantic Ocean (Rodhouse *et al.* 1992b), and in the Indian sector of the Southern Ocean the life cycle of *M. hyadesi* must be closely related to the West Wind Drift, especially in relation to the transport of eggs, larvae, and juveniles (Piatkowski *et al.* 1991). Without some direct knowledge as to where the seals are foraging each year it is difficult to determine whether the changes in relative importance of particular cephalopod species, such as the absence of *M. hyadesi* from the 1987-1988 diet (Green and Burton 1993), reflect a change in relative abundance of prey species or a change in distribution of either the prey species or the foraging areas of the seals.

#### 4.4.4 Age differences

The most important prey, numerically at least, of juvenile seals were *G. antarcticus*, *Mastigoteuthis* sp.? and *M. hyadesi*. Of these, *M. hyadesi* dominated in terms of biomass, but was only a minor component of the adult diet (Table 4.3). Similarly, *T. filippovae* was a common prey of juveniles in terms of biomass but was not eaten by adults. It is possible that these differences were due to the timing of samplings which were constrained by haulout patterns of the various gender and age classes. However, because the diet of females was roughly the same over different seasons, it seems unlikely that the difference in juveniles is entirely due to season. Although there was some overlap in the adult and juvenile diets (Fig.

4.1) juveniles tended to take smaller specimens of most of the species in common (Table 4.5, Fig 4.2). For example, *G. antarcticus* was eaten by adults and juveniles, but those eaten by juveniles were much smaller (Table 4.5).

Juvenile seals, particularly those in their first year, are probably restricted by their ability to capture large specimens of the fast-swimming muscular species, and by their ability to dive deep enough to encounter large prey. There is evidence of vertical descent with ontogenetic development in *A. antarcticus*, *G. glacialis* (Rodhouse *et al.* 1987), and *P. glacialis* (Lu and Williams 1994). Little is known of the diving behaviour of young elephant seals, but 8 to 12 month-old seals have the ability to dive almost as deeply as adults but for only about half as long as adults (Slip 1997).

The smaller proportion of Antarctic cephalopod species in the diet of juveniles than in the diet of adults suggests that while adults fed to the south of Heard Island, juveniles were feeding to the north, possibly closer to the Antarctic Polar Front. This is consistent with the locations of foraging areas as determined by geolocation and water temperature profiles (this volume, Chapter 5, Slip 1997). Thus, near Heard Island juveniles and adults mostly eat similar things.

The ommastrephids *M. hyadesi* and *T. filippovae* may be the largest prey commonly encountered by juvenile seals. Both are muscular squid, and strong swimmers (Roper *et al.* 1985). Little is known of the depth distribution of these species, although *T. filippovae* occurs between the surface and 1000 m depth (Roper *et al.* 1985), and a specimen of *M. hyadesi* was collected in a bottom trawl at 140 m depth over the Kerguelen Shelf to the north of Îles Kerguelen (Piatkowski *et al.* 1991). Thus, it is likely that *M. hyadesi* is common off the Kerguelen Shelf or at the shelf break, including waters relatively close to Heard Island, and at depths easily accessible to juvenile seals. Ommastrephids regularly appear at the surface at night (Clarke 1966), and they are also taken by sub-Antarctic fur seals that do not dive deeper than 250 m (Bester and Laycock 1985).

#### 4.4.5 Comparison with the South Atlantic

As the decline in elephant seal populations in the Indian and Pacific sectors of the Southern Ocean has not been recorded in the South Atlantic sector, and if the decline is in some way food related, a comparison of the diets of these populations might show some informative differences. In general, the species composition of cephalopods at Heard Island was similar to that reported for the prey of elephant seals at South Georgia (e.g., Rodhouse *et al.* 1992a). The major differences were the presence of *M. ingens* and the absence of *Batoteuthis* or *Mesonychoteuthis hamiltoni* in the diet of elephant seals at Heard Island. It may be that in the South Atlantic sector the relative abundance of prey is such that first-year animals have no difficulty locating prey.

#### 4.4.6 Interspecific competition

According to two hypotheses that have been proposed for the population decline of the southern elephant seal, competition is a key factor. One, the direct-competition hypothesis, states that elephant seals have prey species in common with other predators. The other, the overshoot hypothesis, states that the primary prey of elephant seals is largely unexploited by noncongeners. Hindell *et al.* (1994a) argued that the deep foraging dives documented for this species were evidence supporting the latter hypothesis. However, little is known of the biology of the ziphiid odontocete whales, particularly when they are in Antarctic waters. The southern bottlenose whale (*Hyperoodon planifrons*) is a major consumer of cephalopods, and while in Antarctic waters, it feeds on the same squid species as were found in the elephant seal stomachs (Sekiguchi *et al.* 1993, Slip *et al.* 1995). The modal sizes of most prey species common to both were also similar, although whales took larger *G. antarcticus* and *K. longimana*, and smaller *P. glacialis* (Table 4.7). These size differences, particularly for *P. glacialis*, may be due to the time of year samples were taken, and may reflect the growth patterns of this squid. In addition, southern bottlenose whales eat *D. eleginoides*. Thus, the southern bottlenose whale represents a potential competitor with



**Table 4.7:** Estimated modal mantle length (mm) of cephalopods taken by various predators.

Prey Species	Southern elephant seals		Southern bottlenose whales	Sperm whales
	Heard Island <sup>a</sup>	South Georgia <sup>b</sup>	Heard Island <sup>c</sup>	Antarctica <sup>d</sup>
<i>Alluroteuthis antarcticus</i>	153	145	150	181
<i>Chroteuthis</i>	106	135	100	-
<i>Gonatus antarcticus</i>	128	139	214	272
<i>Histioteuthis eltaninae</i>	57	47	46	-
<i>Kondakovia longimana</i>	354	144	470	509
		277		
<i>Martialia hyadesi</i>	190	271	226	-
<i>Moroteuthis knipovitchi</i>	232	237	179	290
				474
<i>Pyschroteuthis glacialis</i>	162	35	91	442
		165		

<sup>a</sup> Present Study

<sup>b</sup> Rodhouse *et al.* (1992a)

<sup>c</sup> Slip *et al.* (1995)

<sup>d</sup> Clarke (1980)

the southern elephant seal, as might other ziphiid odontocetes. The summer population of ziphiid whales in Antarctic waters has been estimated at between 224,000 and 377,000 (Sekiguchi *et al.* 1993), which represents considerable potential competition for squid resources for the southern elephant seal. However, it is not known how much time these whales spend in Antarctic waters, and further studies of diet and geographic and vertical dispersal patterns of ziphiid whales could provide insight into how interspecific competition effects demographic changes in the southern elephant seal.

#### 4.5 ACKNOWLEDGEMENTS

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## CHAPTER 5

### MOVEMENTS, FORAGING AREAS, AND DIVING BEHAVIOUR OF SOUTHERN ELEPHANT SEALS (*MIROUNGA LEONINA*) FROM HEARD ISLAND IN RELATION TO BATHYMETRY AND WATER TEMPERATURE

#### 5.1 INTRODUCTION

The southern elephant seal, *Mirounga leonina*, has a circumpolar distribution in the Southern Ocean and is a major consumer of pelagic fish and squid (Laws 1977). There are four main breeding populations of the southern elephant seal that are centred on South Georgia, the Falkland Islands/Patagonia, Îles Kerguelen and Heard Island, and Macquarie Island, and of these, populations in the Indian and Pacific sectors of the Southern Ocean have decreased in size over the past several decades (Laws 1994). Recent studies using archival or satellite linked time-depth recorders have demonstrated that southern elephant seals disperse from the sub-antarctic islands where they breed and moult, to distant foraging grounds that are often in Antarctic waters (e.g. Hindell *et al.* 1991a, McConnell *et al.* 1992, Bester and Pansegrouw 1992, Slip *et al.* 1994). These studies have examined the free-ranging behaviour of elephant seals from Macquarie Island, South Georgia, and the small population at Marion Island, but little is known of the movements of the populations from Îles Kerguelen and Heard Island. Resights of tagged animals have shown that adult females sometimes move between the two islands, and that some adult males from these populations moult on the Antarctic continent in the Vestfold Hills and at the Windmill Islands (Tierney 1977, Bester 1989, Gales and Burton 1989, Guinet *et al.* 1992). Heard Island and Îles Kerguelen lie on the Kerguelen Plateau which is an extensive area of relatively shallow water (1500 m or less) extending from about 45°S to 60°S and surrounded by an extensive shelf break, in contrast to South Georgia and Macquarie Island where the shelf area is relatively small. The Kerguelen Plateau is a relatively productive area with a commercial fishery existing around Îles

Kerguelen since the 1970's, and there is potential for a small fishery around Heard Island (Williams and de la Mare 1995).

While at sea southern elephant seals must feed intensively in order to acquire sufficient energy reserves to fulfil their energetic requirements for the moulting and breeding fasts. Adult males must acquire sufficient resources to enable them to compete with other males for breeding success, and adult females invest large amounts of resources in a single pup each year over many years. Southern elephant seals are relatively long lived mammals and in order to reproduce successfully they must locate reliable sources of food each year for many years. How they do this is unclear. Biological productivity in the Southern Ocean, and hence the distribution and abundance of prey can be influenced by oceanographic features such as frontal systems and thermoclines, and these can be areas of high biological activity (Lutjeharms *et al.* 1985, Priddle *et al.* 1988). Boyd and Arnborn (1991) suggested that seals concentrate activity at thermal discontinuities in the water column either because seals use changes in water temperature as indicators of where prey might be or because prey naturally accumulate at discontinuities. McConnell *et al.* (1992) suggested that at South Georgia, because the local shelf area contains insufficient prey to sustain the local breeding population, southern elephant seals migrate to areas where food is reliably associated with easily relocatable oceanographic features, such as the Antarctic continental shelf, and the Antarctic Polar Front, and that these areas are in the long term more productive than pelagic meandering.

Although the diet of the southern elephant seal from around their haulout sites has become better known in recent years (e.g. Rodhouse *et al.* 1992a, Green and Burton 1993, Slip 1995), little is known of the diet during the time seals are away from the haulout sites, and this limits our understanding of the foraging ecology of the southern elephant seal. However, identifying the major foraging areas in relation to oceanographic features, and integrating this information with diving behaviour and the distribution of potential prey will

provide a basic knowledge of the foraging ecology of the southern elephant seal, and also provide insights as to how food availability and large scale oceanographic fluctuations might regulate southern elephant seal populations (Hindell *et al.* 1994a).

Here I describe the location of foraging areas and summarise the dive depths, in order to understand more fully the geographic and vertical dispersion of southern elephant seals that breed and moult on Heard Island. I interpret these patterns in relation to oceanographic features, such as the Antarctic Polar Front (APF), the Kerguelen Plateau and the Antarctic Continental Shelf, to thermal discontinuities in the water column, and to what is known of the distribution of the major cephalopod and fish prey of the southern elephant seal, and assess the potential for spatial overlap with commercial fisheries operations on the Kerguelen Plateau.

## 5.2 MATERIALS AND METHODS

I attached micro-processor based location time depth recorders (= GLTDRs, Wildlife Computers, Redmond, Washington, U. S. A.), and VHF transmitters (Advanced Telemetry Systems, Minnesota, USA) to the backs of southern elephant seals at Heard Island, Southern Ocean (53° 05' S, 73° 30' E) using quick setting epoxy (Araldite K268 road-marker adhesive, Ciba Geigy). I deployed GLTDRs on 16 adult females and 17 adult males at the end of their annual moult (females: March, 1992; males: April, 1992) and on 10 adult females at the end of breeding (November, 1992), and retrieved the recorders when the seals next returned to Heard Island several months later. Seals were immobilised using a combination of 50:1 ketamine : diazepam (see Woods *et al.* 1994). Females were weighed using a stretcher, tripod and electronic balance. The mass of males was estimated from snout-tail length (STL) and girth (G) multiple regression relationships (R. Woods unpublished data).

I programmed GLTDRs to record depth every 30 seconds, sea surface temperature every 180 seconds for the entire period that the seals were at sea. Depth was recorded on two

channels; the first operated between 0 and 450 m with an accuracy of  $\pm 2$  m, and the second from 450 to 1500 m with an accuracy of  $\pm 6$  m. Water temperature was recorded on the third channel and was accurate to  $\pm 0.2$  °C. Whenever seals were within 30 m of the sea surface, ambient light was measured every 30 seconds and the highest light level measured every 15 minutes or each time a seal surfaced was recorded in memory. The GLTDRs could archive 512 or 1024 Kbytes of data. I programmed the 512Kb GLTDRs to duty cycle for 30 days of recording followed by a non-recording period of 25 days, so that data spanned the full interval during which seals were at sea. Larger memory GLTDRs, and those deployed on females at the end of breeding recorded continuously. I used software provided by Wildlife Computers to summarise the dive data and describe general features of each dive including dive duration, and maximum dive depth. I determined the daily latitudinal locations of each seal by calculating day length, and longitude from local apparent noon time, using daylight profiles and navigational algorithms as described by DeLong *et al.* (1992). I confirmed or corrected the latitude of these locations by comparing GLTDR recorded sea surface temperature with other measures of sea surface temperature (e.g. Gordon and Molinelli 1982). No latitudes could be calculated around the equinoxes, and these positions were estimated from sea surface temperature. The theory of determining locations from daylight profiles and factors that affect accuracy are discussed fully elsewhere (DeLong *et al.* 1992, Hill 1994). The algorithm provides a range of possible latitudes and longitudes, and the geographic centre of this range is provided to simplify plotting. There is equal probability of the seal being at any point within the range.

To remove locations with potential error due to for example, poor light resolution at dawn and dusk, an iterative forward/backward averaging filter following McConnell *et al.* (1992) was applied to each daily location. A velocity  $V_i$  was determined for the  $i$ th location where  $v_{i,j}$  is the velocity between successive locations  $i$  and  $j$ , such that:

$$V_i = \frac{1}{4} \sum_{j=-2, j \neq 0}^{j=2} (v_{i,j+1})$$

Locations with  $V_i$  greater than the estimated maximum velocity of a seal (2 m/s for adult females, 2.5 m/s for adult males) were adjusted within the confidence limits of the geolocation algorithm and the filter was reapplied. The process was continued until  $V_i$  was less than 2 m/s, or if the location could not be adjusted within the resolution of the algorithm then the location was rejected.

To examine changes in the average rate of travel during the interval at sea, I calculated average velocity over the first nine days at sea, for nine days in the middle of the recording period, and for the last nine days of recording for each seal. The last nine days of recording represented the last nine days before arriving at Heard Island for post breeding females, but post moulting animals were still at their foraging areas. I tested for significance using a two factor ANOVA with sex and periods as the factors, for post moult animals, and a single factor ANOVA with period as the factor for post breeding females.

To examine the influence of sea temperature on diving behaviour I extracted temperature data to establish a sea temperature profile for three periods of six days for each post moult female and male. I chose an interval of six days in order to integrate enough temperatures to determine an average temperature-depth profile without obscuring fine scale changes as the seals moved greater distances. Seals travelled on average about 175 km over six days, although not in a single direction so the temperatures were integrated over an area of less than 100 km by 100 km. I then compared these profiles to frequency distributions of dive depth, and contour profiles of sea ambient temperature to maximum dive depth for each seal over the corresponding period. The three periods were April 12 to 17, June 18 to 23, and July 27 to August 1 for post moult females. For post moult males the periods were May 10 to 15, June 20 to 25, and August 10 to 15. For post breeding females I determined temperature

profiles from December 5 to 10. These periods were chosen as the extent of movements of each individual were similar within each period. For post moult animals the three groups represent autumn foraging within two weeks of leaving Heard Island, early winter foraging, and late winter foraging. For post breeding females the interval is near the middle of the foraging trip.

Statistical analysis were made using SYSTAT (Wilkinson *et al.* 1992).

### 5.3 RESULTS

I recovered GLTDRs from 11 post moult females, seven post moult males, and six post breeding females, and of these, eight GLTDRs from post moult females, five from post moult males, and five from post breeding females contained dive and location records. The GLTDRs from one post moult female and from one post moult male contained incomplete location data due to excessive positive drift in the pressure sensor. Although this depth can be corrected for depth readings, the positive drift caused surface readings to be outside the threshold for recording light. All post moult females gave birth on returning to Heard Island, and all post breeding females had successfully weaned a pup before leaving the island. Although no post moult males achieved beachmaster status on their return to Heard Island four animals ( $STL > 4.10$  m), were regularly sighted on the edge of harems. One male ( $STL = 3.5$  m) left Heard Island much later than the other males and only returned after the breeding season to moult.

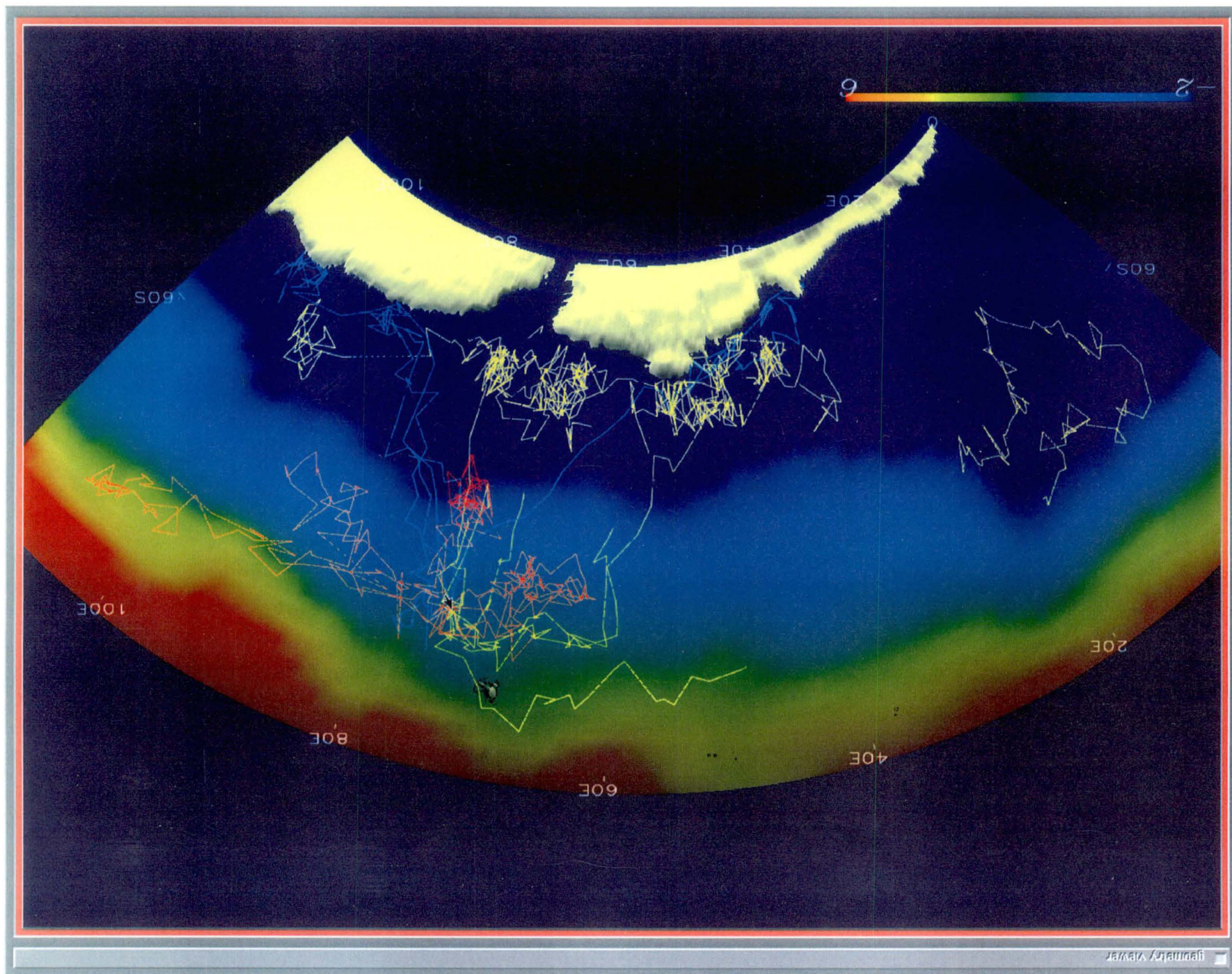
All animals increased in mass over the time at sea (Table 5.1). Mean rate of mass gain was  $1.0 \pm 0.2$  kg/day for post moult females,  $3.4 \pm 1.5$  kg/day for post moult males, and  $1.6 \pm 0.1$  kg/day for post breeding females.

#### 5.3.1 Movement Patterns

Most seals travelled long distances from Heard Island and most of their activity was in relatively cold water south of the Antarctic Polar Front (APF) or in the APF zone (Fig.

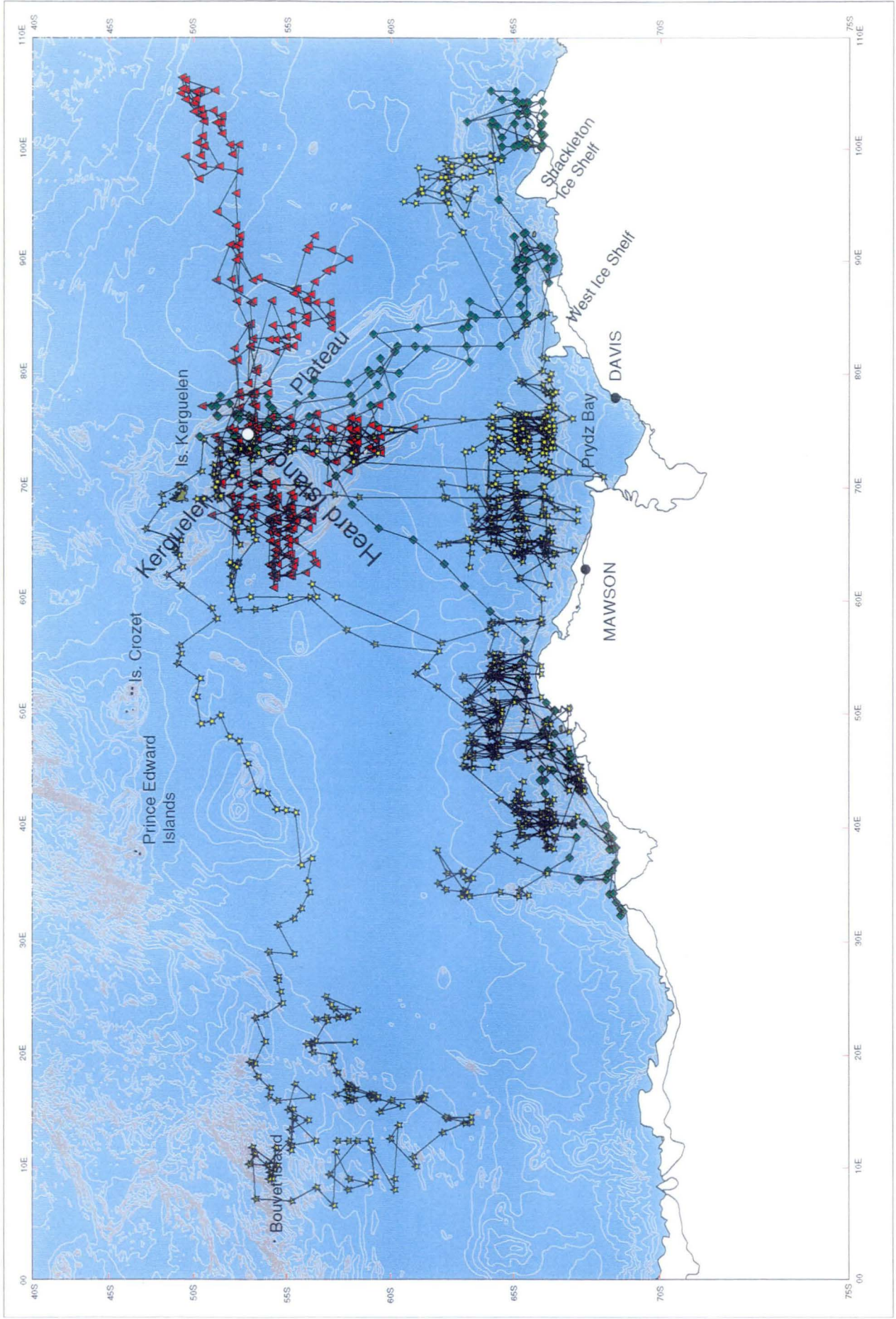


**Fig. 5.1** (overleaf): Average sea surface temperature for the area of the Southern Ocean encompassing the foraging ranges of southern elephant seals from Heard Island. The arrow indicates Heard Island, the land to the north is Îles Kerguelen. The approximate position of the Antarctic Polar Front is represented by the blue-green boundary. Tracks of post moult female elephant seals are plotted in yellow, post moult males are plotted in blue, and post breeding females are plotted in red.



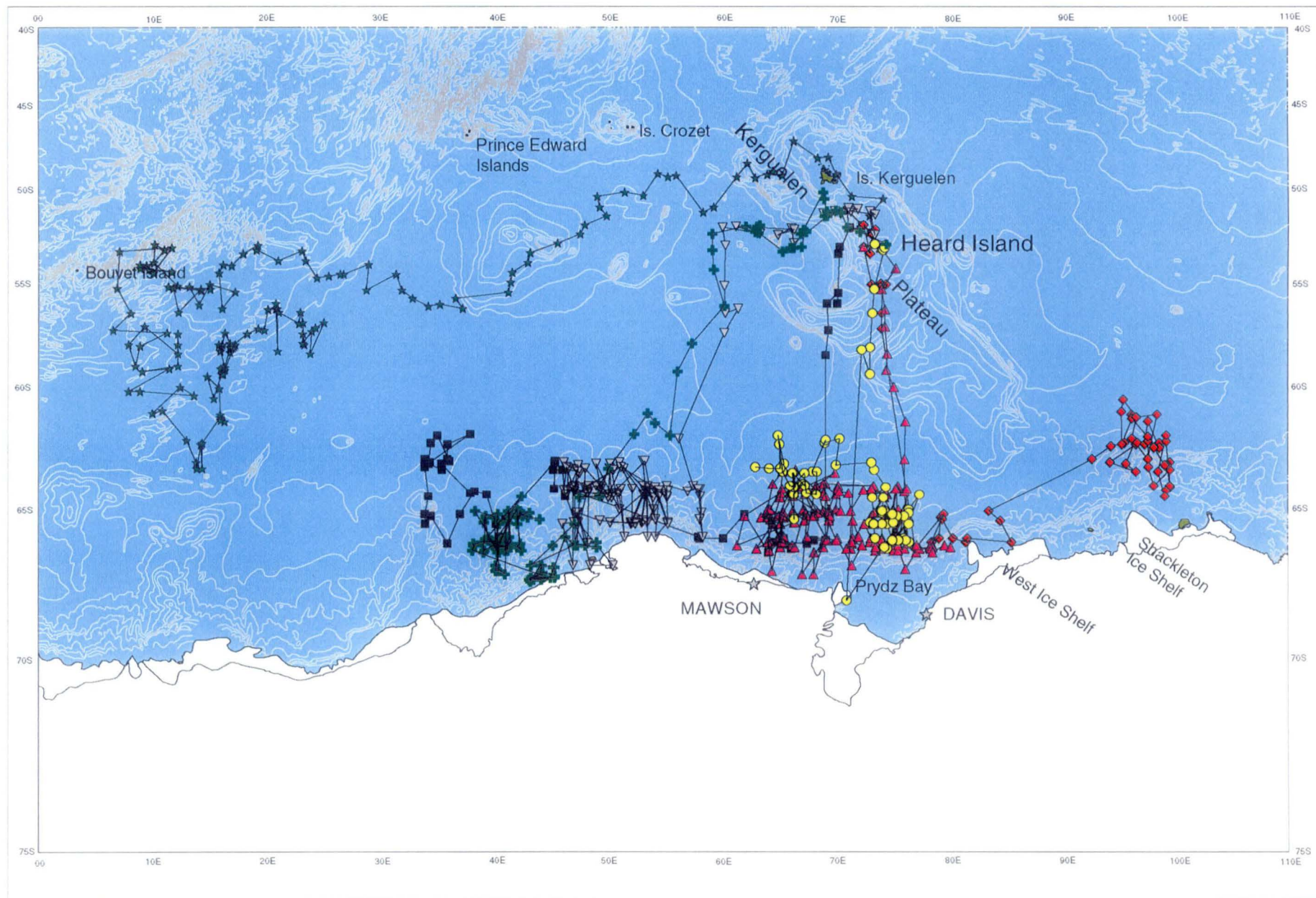
**Fig. 5.2** (overleaf): Movement patterns of southern elephant seals from Heard Island in 1992-93. Post moult female elephant seals are represented by yellow stars, post moult males are represented by green diamonds, and post breeding females are represented by red triangles. Heard Island is indicated with a white spot. Bathymetry represented by the 200 metre contour, then 500 metre contours to 5000 m.





**Fig. 5.3** (overleaf): Movement patterns from March to September 1992 of seven post moult adult female southern elephant seals from Heard Island. Seal numbers are represented by the following: 89-802 black square, 89-807 red diamond, 90-1114 yellow circle, 91-1602 green star, 91-1603 pink triangle, 91-1605 grey triangle, and 91-1607 green cross. Bathymetry represented by the 200 metre contour, then 500 metre contours to 5000 m.





**Table 5.1:** Departure mass, return mass, mean distance travelled per day, maximum distance travelled away from Heard Island, and percentage of time spent over the Kerguelen Plateau for adult male and female southern elephant seals during the post moult (PM) and post breeding (PB) trips to sea.

Seal	Sex	Season	Departure Mass (kg)	Return Mass (kg)	Days at Sea	Mean Distance per Day (km)	Max Distance from Heard Island (km)	% Time over Kerguelen Plateau
91-1602	F	PM	271	546	227	100.7 $\pm$ 62.0	4502	12
91-1603	F	PM	405	574	227	88.6 $\pm$ 53.7	2048	9
91-1604	F	PM	360	525	234			
91-1605	F	PM	306	572	240	91.2 $\pm$ 57.8	2170	11
91-1607	F	PM	286	554	230	76.2 $\pm$ 58.9	2495	28
90-1114	F	PM	321	518	230	84.4 $\pm$ 60.0	1698	18
89-802	F	PM	361	547	235	97.3 $\pm$ 63.9	2652	15
89-807	F	PM	329	572	220	87.9 $\pm$ 53.7	1950	16
87-707	M	PM	1283	1740	156		1575	9
89-810	M	PM	1653	2367	163	90.2 $\pm$ 72.0	2242	10
91-1504	M	PM	1554	2390	155	87.7 $\pm$ 55.0	2836	8
91-1505	M	PM	1913	2058	57	132 $\pm$ 64.4	1759	28
87-706	M	PM	1398	1866	262	86.0 $\pm$ 64.8	335	90
93-1504	F	PB	320	410	58	115.5 $\pm$ 66.7	1258	45
93-1505	F	PB	306	420	84	94.6 $\pm$ 62.9	885	100
93-707	F	PB	324	460	77	156.5 $\pm$ 90.3	2320	26
93-1119	F	PB	328	412	56	103.0 $\pm$ 55.0	632	95
90-1120	F	PB	282	376	62	90.1 $\pm$ 46.0	834	95
Mean $\pm$ sd	F	PM	330 $\pm$ 44	551 $\pm$ 22	230.4 $\pm$ 6.1	89.5 $\pm$ 3.07	2502 $\pm$ 939	16 $\pm$ 6
Mean $\pm$ sd	M	PM	1560 $\pm$ 243	2084 $\pm$ 292	158.6 $\pm$ 72.5	99.0 $\pm$ 11.04	1749 $\pm$ 929	29 $\pm$ 35
Mean $\pm$ sd	F	PB	312 $\pm$ 19	416 $\pm$ 30	67.4 $\pm$ 12.4	111.9 $\pm$ 11.96	1186 $\pm$ 673	72 $\pm$ 34

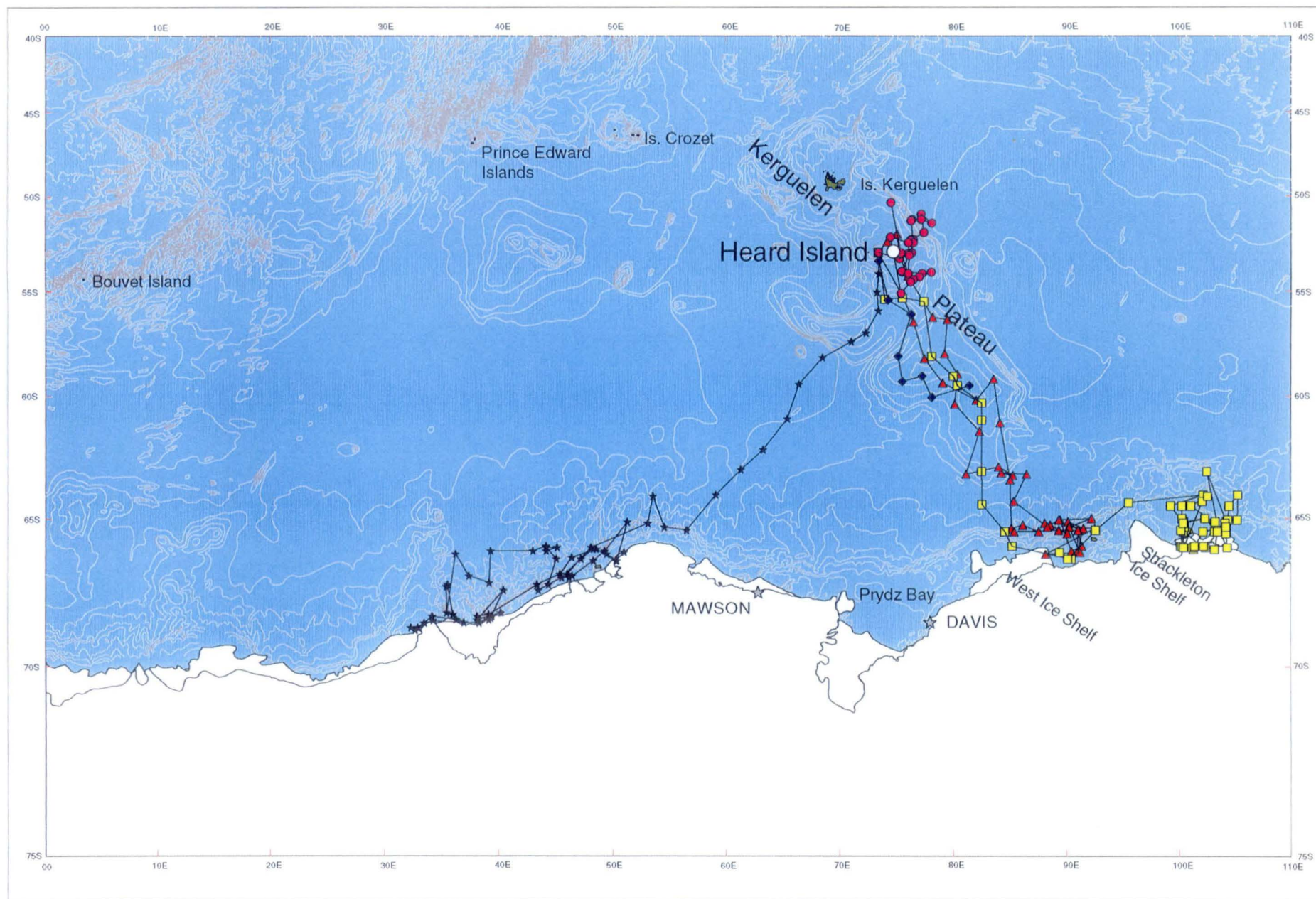
5.1). Adult males and adult females concentrated their activity on different areas, and adult females after the moult moved to different areas than adult females after breeding (Fig. 5.2). Most adult females moved south after the moult and concentrated their activity in relatively discrete areas (Fig. 5.3). These areas were located in pelagic waters in the pack ice zone, with some animals occasionally moving close to the Antarctic continental shelf. Four seals were located relatively close to each other in an area near the western edge of Prydz Bay. The post moult female for which little location data were recorded (91-1604) also travelled into cold water in the pack ice zone where surface temperatures were about  $-1^{\circ}\text{C}$ . Only one post moult female did not move south of  $60^{\circ}\text{S}$  (Fig 5.3). This animal remained close to but mainly south of the Antarctic Polar Front, and travelled the greatest distance away from Heard Island (Table 5.1). Post moult females travelled further from Heard Island than other animals, averaging a maximum distance of  $2502 \pm 939$  km. All post moult females moved in excess of 1700 km away and one travelled 4502 km from Heard Island.

Post moult males migrated further south than females, with four of five males remaining south of  $65^{\circ}\text{S}$  for most of the recording period (Fig. 5.4). The locations of these four males were closely related to the narrow Antarctic continental shelf with most locations occurring where depths were less than 1000 m. Post moult males travelled a mean maximum distance of  $1749 \pm 929$  km away from Heard Island, with four animals travelling in excess of 1500 km (Table 5.1). The younger male travelled a maximum distance of 335 km away from Heard Island and remained near the southwestern edge of the Kerguelen Plateau.

Post breeding females remained north of  $61^{\circ}\text{S}$  for the entire period at sea, with locations occurring either at the south west edge of the Kerguelen Plateau or in pelagic waters to the east of Heard Island (Fig. 5.5). Some animals moved to the edge of the Kerguelen Plateau and concentrated activity in this region with dives following the edge of the plateau (Fig. 5.6). Females travelled a mean maximum distance of  $1186 \pm 673$  km away

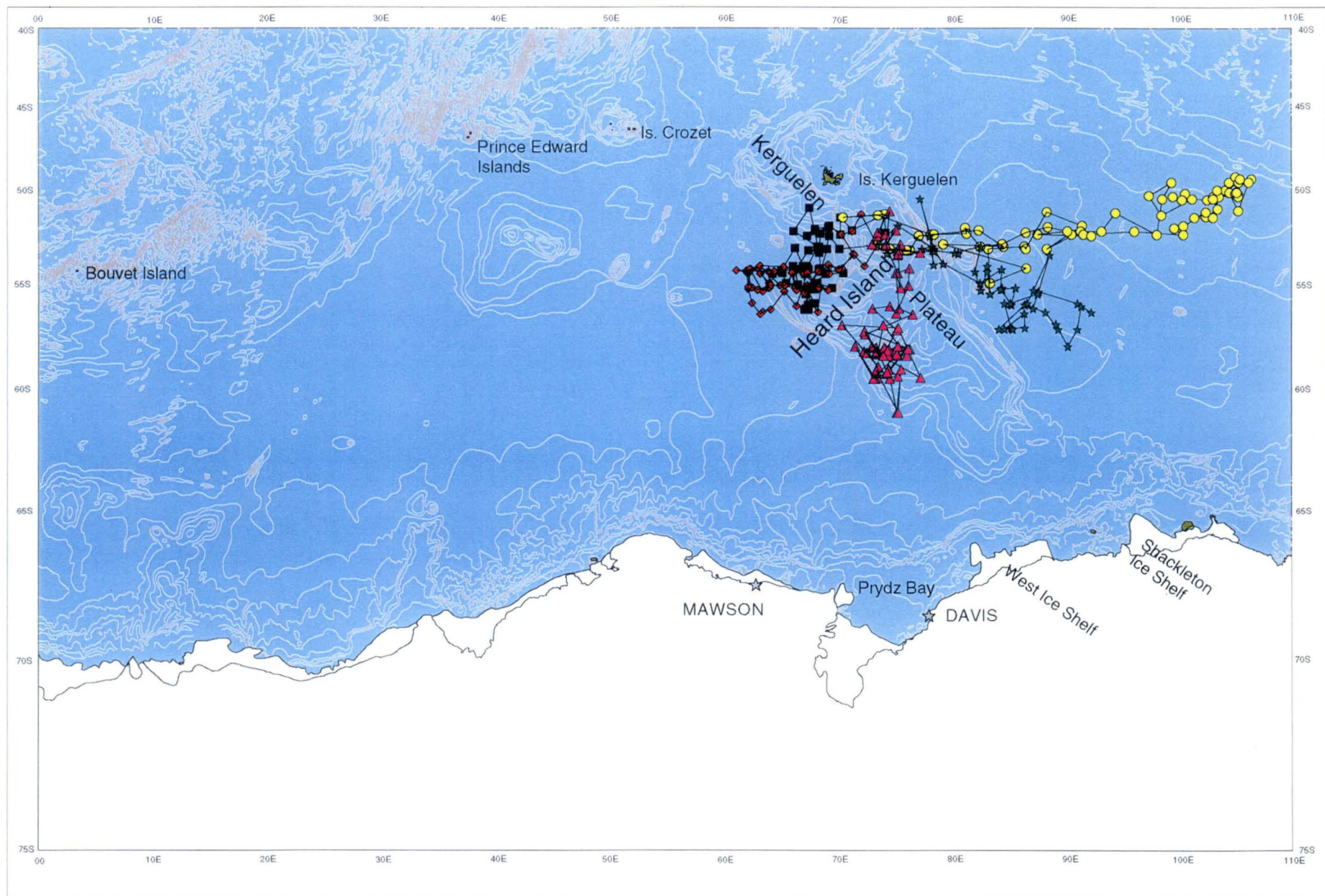


**Fig. 5.4** (overleaf): Movement patterns from April to August 1992 of five post moult adult male southern elephant seals from Heard Island. Seal numbers are represented by the following: 87-706 pink circle, 87-707 dark blue diamond, 89-810 yellow square, 91-1504 black star, and 91-1505 red triangle. Bathymetry represented by the 200 metre contour, then 500 metre contours to 5000 m.



**Fig. 5.5** (overleaf): Movement patterns from November 1992 to January 1993 of five post breeding adult female southern elephant seals from Heard Island. Seal numbers are represented by the following: 90-1119 black square, 91-1120 red diamond, 93-707 yellow circle, 93-1504 green star, and 93-1505 pink triangle. Bathymetry represented by the 200 metre contour, then 500 metre contours to 5000 m.





**Fig. 5.6** (overleaf): Three dimensional representation of diving behaviour of a post breeding adult female elephant seal (90-1120) from Heard Island. The seal was located over the edge of the Kerguelen Plateau to the south west of Heard Island (indicated by an arrow). This plot represent seven days of diving between 20 and 27 December, 1992.





from Heard Island during the post breeding period with three seals travelling less than 900 km away, and one seal travelling over 2000 km (Table 5.1).

There was considerable individual variation in foraging areas among seals (Fig. 5.3-5.5). Although two post moult females and two post breeding females overlapped in their ranges, the temporal overlap in range was small. For six days in June the two post moult females were calculated to be less than half a degree of latitude and longitude away from each other at a point 1325 km away from Heard Island, and for one day in November two post breeding females were within 20 minutes of latitude and longitude from each other at a point 450 km away from Heard Island.

The average proportion of time at sea that was spent on the Kerguelen Plateau was 16% (range 9 to 28%) for post moult females, 72% (range 26 to 100%) for post breeding females, and 29% (range 8 to 90%) for post moult adult males (Table 5.1).

### 5.3.2 Rate Of Travel

All seals had highest rates of travel immediately after leaving Heard Island (Table 5.2). Two factor analysis of variance revealed a significant interaction between sex and period ( $F_{2,24} = 5.020$ ,  $p = 0.015$ ). A *post hoc* Tukey's test revealed that both males and females travelled significantly faster during the first period at sea than at other times (females  $1.24 \pm 0.73$  m/sec, and males  $1.87 \pm 0.79$  m/sec), and that males travelled significantly faster than females during the first period at sea, but not at other times. For post breeding females, analysis of variance revealed significant differences in rate of travel among periods ( $F_{2,12} = 12.319$ ,  $p = 0.001$ ). Tukey's test revealed all periods to be significantly different, with the fastest rate of travel in the first period and the slowest rate of travel in the second period.

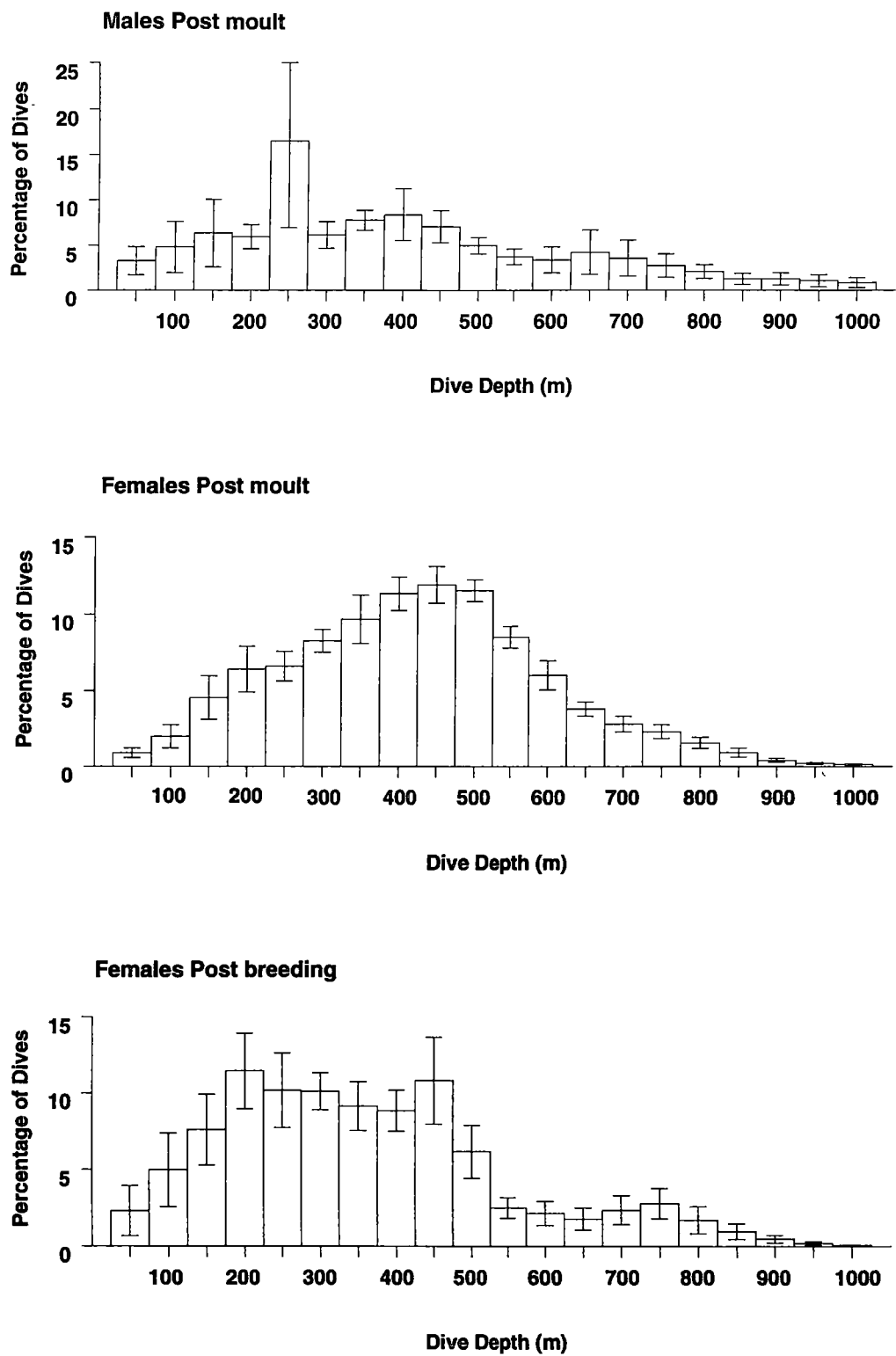
### 5.3.3 Dive Depth

During most dives seals descended rapidly to a specific depth and stayed at or around that depth before ascending rapidly. I use the maximum depth of each dive to represent an

**Table 5.2:** Rate of travel of adult male and female southern elephant seals for three 9 day periods during the post moult (PM) and post breeding (PB) migrations. Period 1 was the first 9 days of travel after each seal left Heard Island, period 2 was 9 days mid-migration, period 3 was the last 9 days that were recorded for each seal, and total represents velocity of the entire period of recording. Period 1 is missing from male 87-706 as this animal remained ashore longer than the other seals and left the island when the GLTDR was duty cycled off.

Seal	Sex	Class	Rate of Travel (m sec <sup>-1</sup> )			
			Period 1	Period 2	Period 3	Total
91-1602	F	PM	1.78 ± 0.60	1.10 ± 0.61	0.85 ± 0.77	1.16 ± 0.71
91-1603	F	PM	0.82 ± 0.57	0.52 ± 0.55	0.64 ± 0.36	1.0 ± 0.61
91-1605	F	PM	0.95 ± 0.43	1.24 ± 0.65	0.70 ± 0.36	1.0 ± 0.68
91-1607	F	PM	1.23 ± 0.49	1.13 ± 0.48	0.43 ± 0.27	0.87 ± 0.68
90-1114	F	PM	1.34 ± 0.84	0.78 ± 0.45	0.93 ± 0.64	0.96 ± 0.69
89-802	F	PM	1.42 ± 0.97	0.96 ± 0.51	0.89 ± 0.61	1.1 ± 0.75
89-807	F	PM	1.12 ± 0.81	0.91 ± 0.56	1.01 ± 0.65	0.98 ± 0.64
89-810	M	PM	1.90 ± 0.90	0.56 ± 0.33	0.59 ± 0.36	1.0 ± 0.84
91-1504	M	PM	1.34 ± 0.51	0.60 ± 0.33	1.00 ± 0.66	1.0 ± 0.65
91-1505	M	PM	2.34 ± 0.63	0.86 ± 0.35	1.59 ± 0.75	1.48 ± 0.76
87-706	M	PM		0.89 ± 0.44	1.01 ± 0.48	1.0 ± 0.75
93-1504	F	PB	2.00 ± 1.10	1.05 ± 0.75	1.35 ± 0.90	1.33 ± 0.77
93-1505	F	PB	1.74 ± 1.02	1.00 ± 0.60	1.03 ± 0.46	1.09 ± 0.73
93-707	F	PB	1.83 ± 0.80	1.10 ± 0.45	1.28 ± 0.49	1.81 ± 1.04
93-1119	F	PB	1.40 ± 0.49	0.95 ± 0.39	1.37 ± 0.64	1.12 ± 0.55
90-1120	F	PB	1.24 ± 0.60	0.69 ± 0.50	1.25 ± 0.52	1.04 ± 0.53
Mean (±SE)	F	PM	1.24 ± 0.73	0.95 ± 0.57	0.77 ± 0.55	1.01 ± 0.04
Mean (±SE)	M	PM	1.87 ± 0.79	0.67 ± 0.35	0.98 ± 0.59	1.12 ± 0.09
Mean (±SE)	F	PB	1.64 ± 0.84	0.96 ± 0.54	1.26 ± 0.60	1.28 ± 0.12





**Fig. 5.7:** Frequency distribution of maximum dive depths for adult female and male southern elephant seals from Heard Island during the post moult season and adult females during the post breeding season. Histograms represent population means of all seals and error bars are standard errors of the population means.

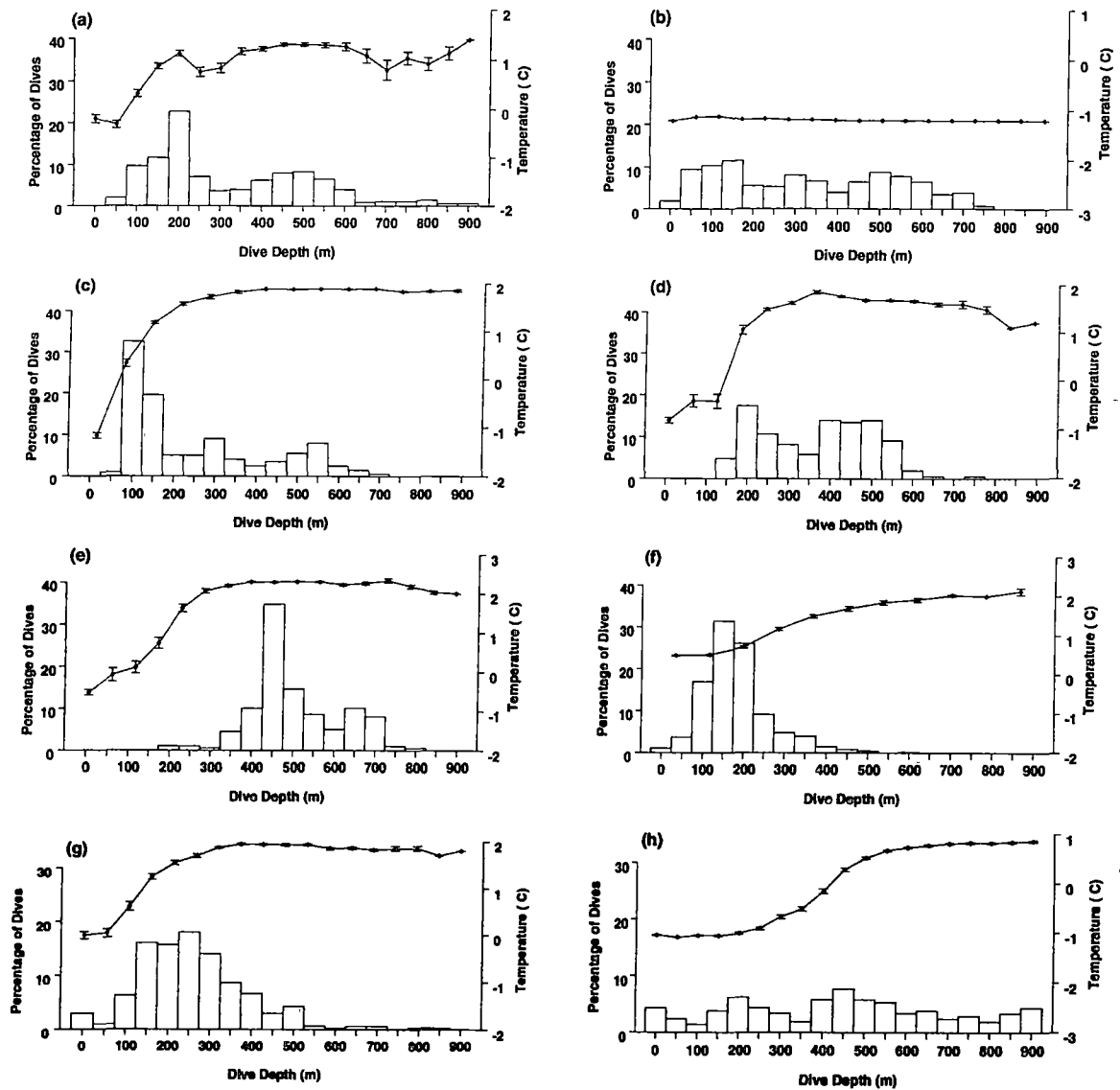
index of vertical dispersion because for most dives, at least one third of each dive was spent at or near the maximum depth. Few dives were shallower than 150 m (post moult females 2.8%, males 8.1%, post breeding females 7.3%), and most dives were between 200 and 800 m (Fig. 5.7).

For post moult females approximately 45% of dives were between 350 and 550 m, and only 1.5% of dives were greater than 850 m. Post breeding females had approximately 41% of dives between 200 and 400 m, and only 1.9% of dives greater than 850 m. Post moult males had a greater proportion of deep dives than females with 5.2% of dives deeper than 1000 m, but most dives were much shallower with 39% of dives between 250 and 450 m.

#### 5.3.4 Sea Temperature

Figure 5.8 shows examples of the relationship between modal dive depth and the mean temperature of the water column while Fig. 5.9 shows the same data plotted over time showing maximum dive depth superimposed on sea temperature. There was a diurnal pattern in dive depth with shallower dives occurring at night. The depths of the shallower dives were sometimes strongly related to temperature changes in the water column (e.g. Fig. 5.9c, d, and f), sometimes only weakly related (e.g. Fig. 5.9a and g), and sometimes unrelated (e.g. Fig. 5.9b, e, and h).

There were two general types of sea temperature-depth profiles recorded from seals south of 55°S: a cold surface layer down to about 100m followed by a transition zone where temperatures increased relatively rapidly from one to three degrees to the warmer Antarctic bottom water (eg. Fig. 5.8a, c, e; Fig. 5.9a, c, e), and a flat profile where little change in temperature occurred, with very cold water extending down to over 1000 m (eg. Fig. 5.8b, Fig. 5.9b). For seals which were north of 55°S two profiles were also recorded: warm surface water extending to about 200 m, followed by a transition zone of about 100 to 200 m where temperatures increased slightly then fell one to two degrees to cooler water below (eg.



**Fig. 5.8:** Sea temperature in relation to depth and the percent frequency of depth of dives for:

(a) Post moult female (89-802) from April 12 to 17 that concentrated diving near the transition of cold surface water and the warmer layer below;

(b) Post moult female (91-1603) from April 12 to 17 with distribution of dive depth not related to sea temperature changes;

(c) Post moult female (91-1603) from June 18 to 23 that concentrated diving activity at the transition between cold surface water and Antarctic Bottom Water;

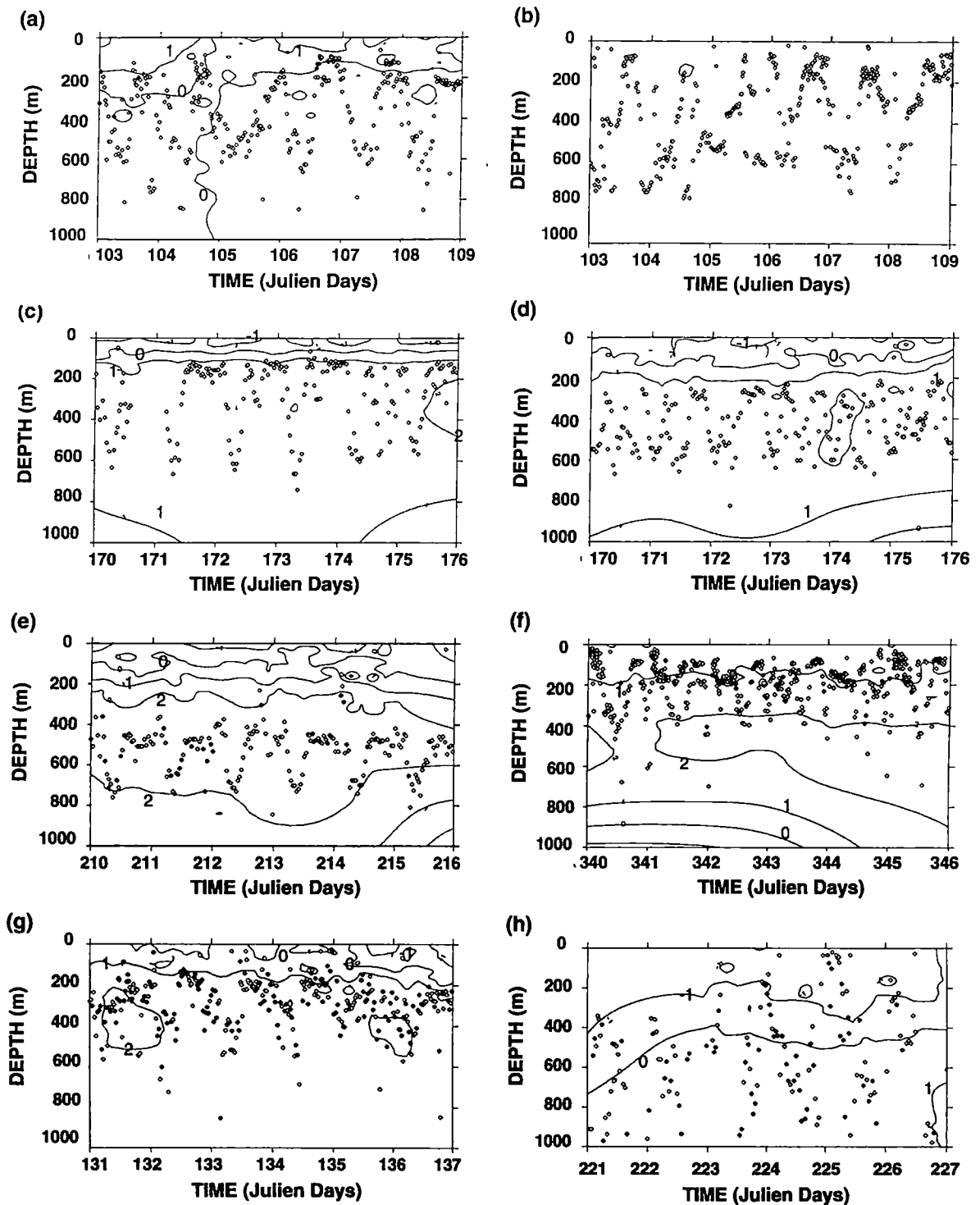
(d) Post moult female (91-1605) from June 18 to 23 that concentrated diving activity in relatively warmer water with some dives close to the transition zone;

(e) Post moult female (91-1607) from July 27 to August 8 that concentrated diving activity in the warmer Antarctic Bottom Water with little activity near the transition zone;

(f) Post breeding female (90-1119) from December 5 to 10 that concentrated diving activity at the transition zone;

(g) Post moult male (87-707) from May 10 to 15 that concentrated diving activity in the transition zone;

(h) Post moult male (91-1504) from August 10 to 15 that showed no relation between the peak of diving activity and sea temperature.



**Fig 5.9:** Maximum dive depths plotted over sea temperature contours over six day intervals with time as universal time for:

- (a) Post moulting female (89-802) from April 12 to 18 showing some diving around temperature discontinuities;
- (b) Post moulting female (91-1603) from April 12 to 18 diving in relatively uniform water of about  $-1^{\circ}\text{C}$ ;
- (c) Post moulting female (91-1603) from June 18 to 24 showing a diurnal pattern of shallower dives near the thermocline;
- (d) Post moulting female (91-1605) from June 18 to 24 showing diving activity concentrated in the warmer mid layer,
- (e) Post moulting female (91-1607) from July 28 to August 3 showing diving activity concentrated in the warmer Antarctic Bottom Water with little activity near the thermocline,
- (f) Post breeding female (90-1119) from December 5 to 10 showing a diurnal pattern of shallower dives near the thermocline;
- (g) Post moulting male (87-707) from May 10 to 16 showing some shallower dives near the thermocline;
- (h) Post moulting male (91-1504) from August 8 to 14 showing no relation between dive depth and temperature contours

Fig. 5.8f, Fig. 5.9f), and flat temperature profiles with temperatures of about 2°C from the surface to over 1000 m.

Five general geographic regions in which seals were located were recognised. They were the Kerguelen shelf zone, the APF zone, the pelagic zone south of the APF, the pack ice zone, and the Antarctic continental shelf zone. There were three general positions in the water column where seals concentrated their diving activity. These were areas of thermally stable water (both relatively warmer at about 3°C and relatively cooler at about -1°C), the transition zone where temperatures changed relatively rapidly, and the warmer deep Antarctic bottom water. During the autumn period modal dive depths of three post moult females which were located in the pack ice or near the Antarctic continental shelf (Table 5.3), occurred in the transition zone (Fig. 5.8a). The other five post moult females were located in the pack ice zone or the Antarctic Polar Frontal zone and modal dive depths occurred in stable water masses (Fig. 5.8b, Fig. 5.9b). In the early winter period two females which were located in the pack ice had modal dive depths in the transition zone (Fig. 5.8c, Fig. 5.9c), while five females which were located in the pack ice or near the Antarctic continental shelf had modal dive depths in the warmer deep water but also showed diving activity in the transition zone (Fig. 5.8d, Fig. 5.9d). One female was located in pelagic water near the Antarctic Polar Front zone which was between 2 and 2.5°C from the surface to over 1000 m. In late winter the modal dive depths of all post moult females occurred in warmer Antarctic deep water (Fig. 5.8e, Fig. 5.9e). In summer four of five post breeding females had modal dive depths in the transition zone (Fig. 5.8f, Fig. 5.9f), while the other female was located at about 58°S (Fig. 5.5), and water temperature was relatively stable at about -1°C from the surface to over 1000 metres.

In the autumn period three adult males which were located in the pack ice or the Antarctic continental shelf region had modal dive depths in the transition zone (Fig. 5.8g, Fig. 5.9g), while one adult male which was located near the Antarctic continental shelf had

**Table 5.3:** Modal dive depth (m), position in the water column and location of adult male and female southern elephant seals from Heard Island during the post moult (PM) and post breeding (PB) migrations. The three modal dive depths for post moult animals are (a) autumn, (b) early winter and (c) late winter. Position in water column is the body of water where modal diving activity occurred, stable water did not vary from the surface to 1000 m, warm water was 2°C or above, cold water was -1.8°C, bottom water was Antarctic Bottom Water and was about 2°C, transition zone was the area where the surface water mixed with the lower water mass, and transition and bottom was the area where bottom water mixed with the layer above. APF zone represents the Antarctic Polar Front.

Seal	Sex	Class	Modal Depth (m)	Position in Water Column	Geographic Location
91-1602	F	PM	(a) 350-400	Warm stable water	Pelagic south of APF
			(b) 350-400	Warm stable water	Pelagic south of APF
			(c) 400-450	Bottom water	Pelagic south of APF
91-1603	F	PM	(a) 50-600	Cold stable water	Pack ice zone
			(b) 100-200	Transition Zone	Pack ice zone
			(c) 150-450	Bottom water	Pack ice zone
91-1604	F	PM	(a) 150-450	Cold stable water	Pack ice zone
			(b) 200-400	Transition and bottom	Pack ice zone
			(c) 500-600	Bottom water	Pack ice zone
91-1605	F	PM	(a) 400-450	Cold stable water	Pack ice zone
			(b) 200-550	Transition and bottom	Antarctic shelf zone
			(c) 400-450	Bottom water	Pack ice zone
91-1607	F	PM	(a) 300-350	Warm stable water	APF zone
			(b) 300-350	Transition and bottom	Antarctic shelf zone
			(c) 450-500	Bottom water	Pack ice zone
90-1114	F	PM	(a) 50-200	Transition zone	Pack ice zone
			(b) 400-450	Transition and bottom	Pack ice zone
			(c) 350-400	Bottom water	Pack ice zone
89-802	F	PM	(a) 200-250	Transition zone	Pack ice zone
			(b) 400-500	Transition zone	Pack ice zone
			(c) 450-500	Bottom water	Pack ice zone
89-807	F	PM	(a) 150-500	Transition	Antarctic shelf zone
			(b) 350-650	Transition and bottom	Pack ice zone
			(c) 350-450	Bottom water	Pack ice zone
87-707	M	PM	(a) 150-300	Transition zone	Pack ice zone
			(b) 650-700	Cold stable water	Antarctic shelf zone
			(c) 650-750	Cold stable water	unknown
89-810	M	PM	(a) 550-700	Cold stable water	Antarctic shelf zone
			(b) 800-900	Cold stable water	Antarctic shelf zone
			(c) 350-450	Cold stable water	Antarctic shelf zone
91-1504	M	PM	(a) 50-250	Transition zone	Antarctic shelf zone
			(b) 700-1000	Bottom water	Antarctic shelf zone
			(c) 450-600	Bottom water	Antarctic shelf zone
91-1505	M	PM	(a) 100-150	Transition zone	Antarctic shelf zone
			(b) *	*	*
			(c)		
87-706	M	PM	(a)		Ashore at Heard Island
			(b) 200-250	Warm stable water	Kerguelen shelf zone
			(c) 200-250	Warm stable water	Kerguelen shelf zone
93-1504	F	PB	100-200	Transition zone	Pelagic south of APF
93-1505	F	PB	450-550	Cold stable water	Kerguelen shelf zone
93-707	F	PB	250-350	Transition zone	Pelagic south of APF
93-1119	F	PB	200-300	Transition zone	Kerguelen shelf zone
90-1120	F	PB	350-400	Transition zone	Kerguelen shelf zone

modal dive depth in relatively stable water of about 0°C. During both winter periods three adult males were located over the Antarctic continental shelf and one was located over the shelf of the Kerguelen Plateau and there was no relationship between modal dive depth and sea temperature for these individuals (Fig. 5.8h, Fig. 5.9h).

## 5.4 DISCUSSION

### 5.4.1 Accuracy of Locations

There are several sources of potential error in determining location from light levels such as timing errors, atmospheric thermal and pressure gradients, interpolation errors when the animal is diving at dawn or dusk, excessive movement of the animal between dawn and dusk, and errors in the equations which predict dawn and dusk (Hill 1994). In order to validate the method of determining location from light levels, DeLong *et al.* (1992) collected data from a TDR mounted on a ship, and compared estimated locations with the ships location for days when the ship travelled less than 100 km in a 24 hour period. They found that 43% of estimated locations fell within the predicted zone which was an area of about 110 km x 110 km, and that on other days the actual location was within an average of  $56.7 \pm 28.9$  km. Stewart and DeLong (1995) determined locations for a female northern elephant seal using a satellite transmitter and a light level recorder simultaneously. They estimated satellite transmitter error to be  $21 \pm 43$  km, and found the overall average difference between the two methods was  $67 \pm 31$  km, while on days when the seal travelled less than 50 km average differences were  $32.1 \pm 9.6$  km, and on days when the seal travelled greater than 50 km average differences were  $81 \pm 36.1$  km.

Although I have no way of verifying the locations at sea, all locations while seals were known to be at Heard Island were within the predicted zone which was an area of about 110 km x 180 km. This is consistent with calibrations for the northern elephant seal which suggest that the locations of free ranging seals calculated from light levels and sea temperature are within 1° of latitude and 1° of longitude of their true locations (DeLong *et al.*

1992, Hill 1994, Stewart and DeLong 1995). Errors in predictions of latitude are somewhat less at higher latitudes although locations cannot be calculated around the equinoxes or when there is virtually constant or no daylight (DeLong *et al.* 1992). As animals moved south from Heard Island the size of the predicted zone fell to an area of about 90 km x 120 km.

### 5.4.2 Movement Patterns

Migration to distant foraging areas which are associated with oceanographic features appears to be a general strategy of both southern and northern elephant seals (eg. Hindell *et al.* 1991a, McConnell *et al.* 1992, Fedak *et al.* 1994, Slip *et al.* 1994, Stewart and DeLong 1994, Le Boeuf *et al.* 1993, McConnell and Fedak 1996). Adult southern elephant seals from Heard Island ranged over more than one quarter of the Southern Ocean extending longitudinally from 4°W to 110°W and latitudinally from close to the Antarctic continent at 68°S to pelagic waters around the Antarctic Polar Front at 50°S. However, there were obvious areas of concentrated activity (i) geographically, such as over the shelf breaks of the Antarctic continent and the Kerguelen Plateau, and (ii) in the water column, for example southern elephant seals appear to spend little time foraging in the euphotic zone (< 200 m) and concentrated activity at depths of between 250 and 800 m. These data suggest that most adult males and females migrate south of 60°S following the moult, although a small proportion remain further north, either in pelagic waters near the Antarctic Polar Front (females), or at the edge of the Kerguelen Plateau (males). Moreover, seals migrate relatively quickly to their foraging areas, with males averaging 162 km per day and females 110 km per day during the first week away from Heard Island. When seals were at their foraging grounds the average rate of movement over a week dropped to 58 km per day for males and 66 km per day for females. These rates of travel were faster than those recorded by McConnell and Fedak (1996) from southern elephant seals from South Georgia using satellite relay data loggers. These authors reported a mean distance moved per day of 38km/day over the whole time at sea and 77 km/day during the first ten days at sea for adult females that travelled



similar distances to adult females from Heard Island. These differences may be accounted for by the different techniques used to determine location, as satellite determined locations occur more frequently than once per day and under good conditions can have very small associated errors, while the geolocation determined locations have larger confidence intervals and locations can only be determined once per day. Alternatively these differences may be real as the higher densities of food around South Georgia may mean animals travel more slowly.

Although seals travelled long distances from Heard Island in the winter post moult foraging trip, post breeding females spent 68% of time at sea on the Kerguelen Plateau. In addition, the one smaller male that was tracked remained on the Kerguelen Plateau for the entire post moult foraging trip. This suggests that the Kerguelen Plateau was an important foraging area and that commercial fisheries operating in this area may be competing directly with elephant seals. The Kerguelen Plateau may also be an important foraging area for juveniles as although little is known of the movement patterns of juveniles two first year animals spent most of their time in this region (This volume, Chapter 6).

#### **5.4.3 Relationship of Primary Productivity and Movements of Seals**

Although there was considerable variation in the location of foraging areas among individual seals, some individuals showed overlap in their foraging areas, although the temporal overlap was small. Nonetheless, that two animals during the post moult migration and two animals during the post breeding migration were located close enough such that interactions at sea may have occurred hundreds of kilometres from Heard Island suggests that seals concentrated activity on areas of high biological productivity. Much of the variation in foraging areas may be due to individual experience, and individual seals may return to areas known to be good foraging grounds. McConnell and Fedak (1996) reported that three southern elephant seals from South Georgia that had been tracked over more than one season

were consistent in their general outward route, suggesting that differences in foraging areas among individual seals may be consistent from year to year.

The distribution of the foraging areas of southern elephant seals are probably correlated with areas of high primary productivity. Frontal regions in the Southern Ocean, such as where subantarctic waters and Antarctic waters meet, are known to be areas of biological enhancement, and are favourable for primary and secondary production (Lutjeharms *et al.* 1985). Nototheniid fish such as *Notothenia rossii* and *Dissostichus eleginoides* feeding on plankton and fish are concentrated near oceanic frontal systems (Duhamel 1982). Upwelling (Buckley *et al.* 1979) and frontal systems associated with ice edges (Ainley *et al.* 1984) have been suggested as mechanisms that might enhance local productivity and prey availability and ultimately result in high concentrations of marine predators (Fraser and Ainley 1986). Adult male southern elephant seals were often located close to the Antarctic coast either at the edge of or over the Antarctic Continental Shelf (Fig. 5.4), suggesting that this is a highly productive region, resulting from upwelling associated with the rise of Antarctic Bottom water (see Fig. 5.9e). In addition the boundary between perennial pack-ice and the coastal zone, which is a narrow region of about 50 km width and contains ice shelves, fast ice and polynyas, is a favoured habitat for krill and other metazoans, and is an area used extensively for foraging by penguins (Eicken 1992).

#### 5.4.4 Thermal Structure of the Water Column

The dive depth pattern of seals in this study were not consistently related to the thermal structure of the water column. Boyd and Arnborn (1991) reported that a single adult female southern elephant seal during the first 27 days of the post moult period at sea spent 55-60% of its time between 200 and 400 m, with most dives occurring around the depth associated with the transition to warmer deep water. Three seals in this study showed a similar pattern during the corresponding time period, with some diving activity concentrated at the bottom of the cold surface layer and the top of the warmer deep water (eg. Fig. 5.8a,

Fig. 5.9a). However, the other five seals concentrated activity at depths where temperatures were relatively stable, but these animals were in areas where the warmer Antarctic bottom water occurred at depths greater than 1000 m (eg. Fig 5.8b, Fig. 5.9b). During both winter periods 38% and 25% of seals showed a tendency to concentrate diving about thermal changes in the water column.

Southern elephant seals from Patagonia (Campagna *et al.* 1995), and northern elephant seals (Hakoyama *et al.* 1994) do not appear to use thermal discontinuities to locate prey, and both dive through a steep thermocline when they are near the continental shelf. My data suggest that sometimes southern elephant seals concentrate diving activity at the depths where thermal discontinuities between water masses occur, either using them as a cue to the location of prey or because they act as a ceiling for vertically migrating prey. However, at other times seals dived independently of any thermal discontinuities which may be a reflection of the temporal and spatial patchiness of prey distribution, or they were located where the thermal structure of the water column was relatively homogenous. Moreover, this was relatively independent of geographic location (Table 5.3). Adult female southern elephant seals exhibit a general pattern of diving shallower at night than during the day, and for those seals which showed dive activity at a thermocline, it was often the shallower night time dives which were in this region of the water column (eg. Figs 5.9b, 5.9d, 5.9f). It may be that the vertical migration of prey was limited by thermal discontinuities in the water column, and hence the seals foraged in that region. However, some seals showed a similar diurnal pattern of dive depth that was not related to thermal discontinuities (eg. Fig. 5.9e), suggesting that seals that do forage near the thermocline do so because the prey accumulates there, but do not necessarily use the thermocline as a cue to the location of prey. When adult males were located over the Antarctic continental shelf they often showed dive patterns consistent with benthic foraging (Slip unpublished data), and dive depth was not related to the position of thermal discontinuities (eg. Fig. 5.9h). In winter upwelling of the warmer

Antarctic Bottom Water occurs and seals tended to concentrate activity in this water mass (eg. Fig. 5.9e).

#### 5.4.5 Diet

Studies of the diet of the southern elephant seal at Heard Island through stomach lavaging suggested that their main prey were muscular mesopelagic squid, particularly *Kondakovia longimana*, *Moroteuthis knipovitchi*, *M. ingens*, *Alluroteuthis antarcticus*, *Psychroteuthis glacialis*, and *Gonatus antarcticus*, and nototheniid, channichthyid and myctophid fish (Green and Burton 1993, Slip 1995). As elephant seals digest food relatively rapidly, with mean retention time of digesta in captive seals reported at 13 h (Krockenberger and Bryden 1994), items recovered from animals at Heard Island would have been consumed close to the island. Although there are no data on retention times of hard remains such as squid beaks, McConnell and Fedak (1996) assumed a retention time of 2-3 days. By assuming the same retention rate and using the rate of travel above, food samples lavaged from Heard Island elephant seals would have been taken on the Kerguelen Plateau, within about 200 - 400 km of the island. These samples may not be representative of the diet while seals are in Antarctic waters. However, little is known of the distribution and abundance of cephalopods in the Indian Ocean sector of the Southern Ocean, but many of the species taken within 200 -400 km of the island may also occur in Antarctic waters and be potential prey for elephant seals. Surveys of the cephalopods of Prydz Bay identified the presence of *K. longimana*, found aggregations of *P. glacialis* on or near the bottom close to the edge of the continental shelf, and found *A. antarcticus* occurred both over the shelf and in deep water of the open ocean (Lu and Williams 1994). However, *M. ingens*, *M. knipovitchi* and *G. antarcticus* were not present in Prydz Bay despite being common around Heard Island, which led Lu and Williams to suggest that either these species do not reach Antarctic waters in the Indian Ocean sector, or their presence in Prydz Bay is seasonal, or the absence of these species was due to sampling biases. In the Antarctic there are two trophic groups of squid

which are segregated by species as well as ontogenetically within species: those that feed in the euphotic zone chiefly on krill and zooplankton, and those that feed in the mesopelagic and bathypelagic zones on fish and squid such as *M. knipovitchi*, and large *K. longimana* (Nemoto *et al.* 1985).

Studies of the diet of the southern elephant seal have also identified fish as important prey but it is not possible to determine the relative importance of fish and squid from lavage studies due to differences in rates of digestion. Fish may be at least as important as squid as they are generally higher in energy than squid (see this volume, Chapter 7). The main fish prey identified from southern elephant seal stomachs include mainly nototheniids, channichthyids and myctophids, but the overall diversity of fish identified from lavage studies were less than that of cephalopods (Green and Burton 1993, Slip 1995). There are several mesopelagic and demersal fish which are known to occur in the areas where elephant seals foraged. For example, several nototheniids including *Dissostichus mawsoni* have circumpolar distributions south of about 65°S and is found at depths between 100 and 1600 m (Hureau 1985), and is similar to *D. eleginoides* which has been recovered from stomachs of elephant seals at Heard Island (Slip 1995). Myctophids, which are prey of *M. knipovitchi* (Nemoto *et al.* 1985), only occur in water seaward of the Antarctic Continental Shelf break, while the nototheniid *Pleuragramma antarcticum*, which is also an important prey of some squid species in Prydz Bay, occurs mainly on the continental shelf (Lu and Williams 1994).

#### 5.4.6 Sex Differences in Foraging

Differences in the location of the main foraging areas of males and females probably reflect differences in foraging strategies. Males concentrated activity close to or over the Antarctic continental shelf and showed dive profiles consistent with both benthic and pelagic foraging (unpublished data), while females concentrated activity in pelagic waters, and only occasionally moved over shelf areas where benthic foraging was possible. In northern elephant seals sexual segregation of foraging areas occurs with males ranging more poleward

than females or immature males (Le Boeuf *et al.* 1993, Stewart and DeLong 1993). Adult male northern elephant seals simply transit through the Subarctic Frontal Zone and the eastern North Pacific Transition Zone and Domain (where adult females concentrate their foraging), and focus their foraging in the Subarctic Water Mass, presumably to capitalise on the abundance of large oily gonatid squid which occur there (Stewart and DeLong 1993). Female northern elephant seals forage almost exclusively in pelagic waters while males forage both in pelagic waters and benthically near continental margins (Le Boeuf *et al.* 1993).

During the post breeding period adult females dispersed less than half the distances travelled during the post moult period (Table 1), and remained north of 61°S (Fig. 5.5). During this time the major foraging areas were either in pelagic waters close to the Antarctic Polar Frontal zone or in waters off the edge of the Kerguelen Plateau. Although I have no data for post breeding males, the sex differences which occurred during the post moult migrations probably also occur post breeding. Evidence for this comes from the existence of moult sites on the Antarctic Continent, which are used almost exclusively by adult and immature males, some of which have been resighted at Heard Island during the breeding season (Slip 1993). This suggests that a proportion of the male population forages close to the Antarctic continent during the post breeding period, and some animals do not return to Heard Island for the moult. Those adult males that do return for the moult may forage closer to Heard Island, for example on the southern edge of the Kerguelen Plateau.

The differences in male and female foraging areas in both southern and northern elephant seals may be linked to differences in energy requirements that result from sexual size dimorphism, or differences in their abilities to find and capture prey of various sizes and nutritional content (Hindell *et al.* 1991a, Stewart and DeLong 1993). Male southern elephant seals gained mass at a rate of about 3.5 kg per day while female southern elephant seals gained mass at about 1 kg per day (Table 5.1). To achieve this higher mass gain males may need to locate larger prey. There is a tendency for larger seals to take larger prey for some

squid species (Slip 1995). As ontogenetic descent occurs in cephalopods (eg. Nemoto *et al.* 1985), adult males may be foraging for large prey during the 9% of dives deeper than 850 m. Adult females had less than 4% of dives greater than 850 m during the post moult migration and less than 1% greater than 850 m during the post breeding migration. The location of male foraging areas may depend on the availability of large prey at these depths, and it is likely that large prey occur at higher densities at the edge of the continental shelf than in the open ocean. Alternatively the sex differences in foraging areas may be because males and females take very different prey during this time or using different foraging strategies, which may result from the energetic trade off between the energetic cost of catching prey and the energetic gain from that prey. If seals are maximising energy efficiency then hunting strategies are sensitive to prey swim speeds with slow swim speeds effective for faster moving prey and maximum swim speeds effective for locating slower moving prey (Thompson *et al.* 1993). For example, large adult males may use sit-and-wait foraging, as suggested by Le Boeuf *et al.* (1993) for northern elephant seals, to catch large fast moving prey such as muscular squid, while females may actively search for slower moving schooling prey.

#### 5.4.7 Comparison with Other Populations

The movement patterns of adult seals from Heard Island were similar to what is known of those from the other populations. However, southern elephant seals from other populations have not shown the marked change in foraging areas between the post moult and the post breeding migrations (eg. Hindell *et al.* 1991a, McConnell and Fedak 1996). This may be because the Heard Island population has access to a closer, reliable summer food source associated with the Kerguelen Plateau, than do the South Georgia or Macquarie Island populations. Alternatively, the seasonal differences may merely reflect individual differences in foraging preferences as adult female northern elephant seals tended to range further during the post moult period than during the post breeding period although two of three individuals

which were tracked for a complete yearly cycle followed similar paths in each season (Stewart and DeLong 1995).

Southern elephant seals from Macquarie Island forage in Antarctic waters from about 120°E in the west to the middle of the Ross Sea in the east, and in the Antarctic Polar Frontal Zone from about 140°E to 165°W (Hindell *et al.* 1991a, Antarctic Division, unpublished data). Adult males forage mainly over the shelf regions of both Antarctica (south of 62°S) and the Campbell Plateau employing both benthic and pelagic foraging, while adult females forage pelagically either in Antarctic waters north of the shelf region or in waters near the Antarctic Polar Frontal Zone (Hindell *et al.* 1991b, Slip *et al.* 1994). Southern elephant seals from South Georgia showed two types of migrations: an easterly open ocean route with little correlation to topography was followed by females, and a track closely correlated with the continental shelf either at South Georgia or the Antarctic Peninsula was followed by both males and females (McConnell and Fedak 1996). The only other information for elephant seals from the Heard-Kerguelen sub-population comes from Bester and Pansegrouw (1992) who tracked three post breeding females with GLTDRs from Marion Island to three widely separated areas between 1100 km and 1400 km away. They suggested that the foraging range of elephant seals from Marion Island overlapped with the Îles Crozet population but not with the Îles Kerguelen and Heard Island populations. However, the dispersion of one post moult adult female in the present study (91-1602) included the area used by one of the seals from Marion Island (Fig. 5.4). Elephant seals tagged at Îles Kerguelen and at Heard Island have been sighted at Marion Island but it was not known whether they returned to their island of origin (Bester 1988b, 1989). The present study has demonstrated that animals probably do return to the islands of origin, and that elephant seals sighted at the Ob Bank and Lena Seamount (which the above female also passed by) to the south of Marion Island (Bester 1989), could possibly have come from Heard Island.



The foraging areas of southern elephant seals from Heard Island may overlap with those from South Georgia and those from Macquarie Island. The western most point in the range of the seals in our study was about 4500 km away from Heard Island and about 2500 km away from South Georgia. This is well within the potential range of seals from South Georgia (McConnell and Fedak 1996). The easterly extent of the foraging range of seals in our study was about 2800 km away from Macquarie Island and about 2300 km away from Heard Island. Although elephant seals from Macquarie Island have not been tracked west of about 120°E (Slip *et al.* 1994), an adult male which was tagged during the moult in the Windmill Islands (66°20'S, 110°30'E) was resighted at Macquarie Island during the breeding season (Australian Antarctic Division, unpublished data). This suggests that broad scale changes in the Southern Ocean that influence the distribution and abundance of food might affect all populations of southern elephant seals.

**CHAPTER 6****DIVING AND FORAGING BEHAVIOUR OF JUVENILE SOUTHERN ELEPHANT SEALS  
FROM HEARD ISLAND<sup>1</sup>**

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## CHAPTER 7

### BIOMASS AND ENERGY CONSUMPTION OF THE SOUTHERN ELEPHANT SEAL POPULATION AT HEARD ISLAND

“The elephants spend most of their life at sea, no one knows exactly where.....But their proper area is the roaring forties and further south, right down almost to the antarctic circle. In these stormy waters they live for many months on end without coming to land even for sleeping, and in them they must find a great abundance of food, for they reach an enormous size and fatness.”

*L. Harrison Mathews (1952), Sea Elephant:  
The Life and Death of the Elephant Seal*

#### 7.1 INTRODUCTION

A knowledge of the total food or energy requirements of seal populations is important in understanding the interaction between those populations and the surrounding marine resources. Estimation of food consumption of pinnipeds from a knowledge of the prey ingested is extremely difficult as direct observation of animals feeding is generally not possible and information from stomach contents is of little use in estimating total consumption of food. However, by considering the energy demands of individual seals and by synthesizing available data on growth, reproduction, moult, haulouts, locomotion, and foraging the total energy demand of individual seals can be estimated and then projected onto the age structure and size of the population. This information can be combined with a knowledge of the dietary composition and the energy content of the prey to predict annual food consumption by the population. Further, examining the energy demands of different age and sex classes can help identify which parts of the population are vulnerable to fluctuations

in their food supply or which parts of the population have the greatest impact on resources (Boyd *et al.* 1994).

A commercial fishery has existed on the northern part of the Kerguelen Plateau since the 1970's, but apart from some exploratory fishing, there has been little fishing activity in the southern part of the Kerguelen Plateau which includes the area around Heard Island (Williams and de la Mare 1995). Only two fish species, *Champscephalus gunnari* and *Dissostichus eleginoides*, occur in sufficiently large numbers in the Heard Island region to support a fishery (Williams and de la Mare 1995), and both these species are prey of the southern elephant seal (Green and Burton 1993, Slip 1995). Recently commercial fishing for these two species has begun in the Australian sector of the Kerguelen Plateau.

Previous estimates of food consumption for the Heard Island population of southern elephant seals, and earlier estimates for the South Georgia population have been based largely on crude estimates of consumption per unit biomass (Laws 1977, McCann 1985, Woehler and Green 1992). This approach, while providing an estimate of total consumption, gives little information as to how changes in prey distribution and abundance, or changes in the population size or structure might affect food consumption. The bioenergetic approach has been used to estimate food consumption for southern elephant seals at South Georgia (Boyd *et al.* 1994), harp seals (*Phoca groenlandica*) in the north-west Atlantic (Lavigne *et al.* 1985), and grey seals in the North Sea (Hammond and Fedak 1994).

The objectives of this paper were to: (1) synthesize recent information about diet, foraging ranges and energetics of the southern elephant seal by considering energy consumption of the Heard Island population; (2) examine changes in energy demands in relation to age and sex; and (3) indicate possible areas of interaction between southern elephant seals and commercial fisheries in the Indian Ocean sector of the Southern Ocean.

## 7.2 METHODS

### 7.2.1 Population Parameters, Growth and Biomass

#### 7.2.1.1 Survival Rate

I determined survival rate for females based on cross-sectional age distributions obtained from teeth. I chemically immobilised 130 adult females during the moult with a combination of ketamine and diazepam soon after they came ashore at Heard Island in January and February 1992 by intramuscular injection via a long plastic tube (Woods *et al.* 1989). Once seals were immobilised I removed a lower left incisor using dental elevators and the method described by Arnbom *et al.* (1992). I weighed seals using a stretcher, tripod and electronic scale, and took standard length and girth measurements. Teeth were stored in 10% alcohol and returned to Australia. Teeth were set in epoxy resin and sectioned using a diamond edged circular saw (Falcon Enterprises Co. Taya, Taichung, Taiwan) to a thickness of 0.4 ml. Sections were polished using wet-dry paper, then etched for 120 to 150 minutes in a bath of EDTA. They were then coated with gold and viewed using a scanning electron microscope. Images were counted three times by one investigator and twice by another with no knowledge of previous counts. Age determination was consistent between counts with 8% of counts varying by one year and less than 1% of counts varying by two years. One year was assumed to be equivalent to a growth layer group of one dark and one light band (McCann 1980). The technique was validated against five animals of known age, representing ages 3 to 7 years.

Survival rate ( $l_x$ ) of females was calculated for age classes of 3 years and above from the stationary age distribution using a log-polynomial smoothing formula (Caughley 1977). I assumed longevity for females to be 23 years (Hindell and Little 1988). To determine survival of 3 year olds and under, I assumed pup production was unchanged between 1991 and 1992, and used population estimates of yearlings and 2-3 year olds at the moult (this volume, Chapter 3). To separate the counts of 2 and 3 year olds I used the estimate of 3 year

old survivorship from animals that were aged from teeth. I assumed pregnancy rates of 26.2%, 56.5%, and 76.3% for 3, 4 and 5 year olds respectively (Bester and Wilkinson 1994), and 96% for females 6 years and over (Australian Antarctic Division, unpublished data). For males I based survivorship on life tables from South Georgia McCann (1985), and modified them for the first three years using the haulout counts from Spit Bay. I assumed pre-weaning mortality to be 2.5 % (this volume, Chapter 3).

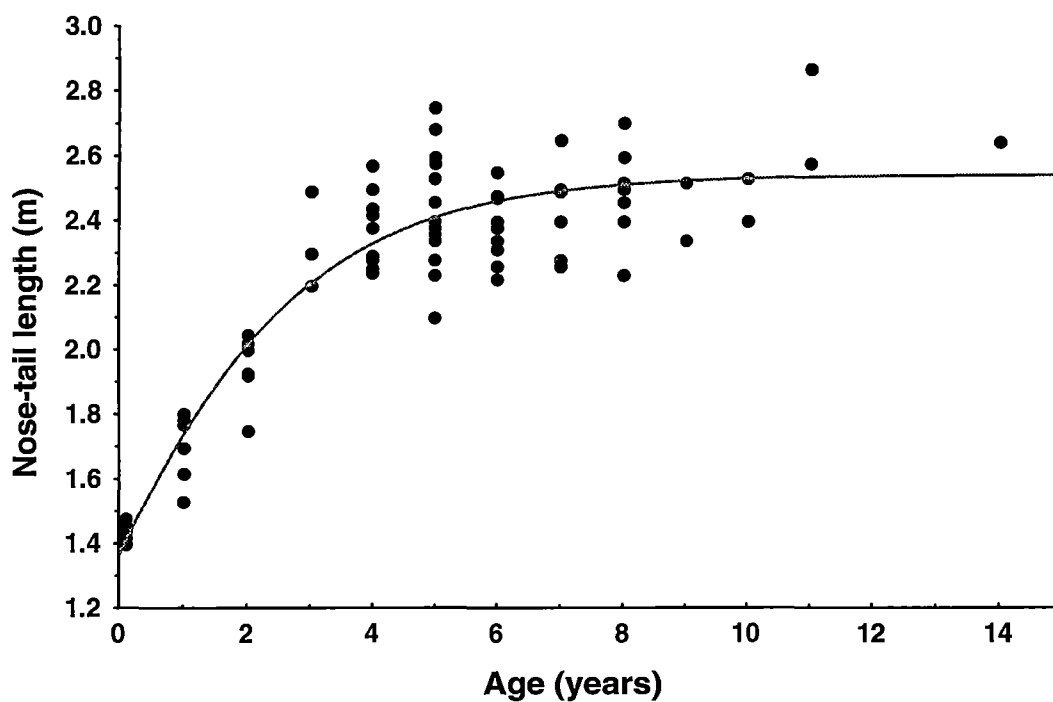
#### 7.2.1.2 Growth

For the purposes of this analysis I follow Boyd *et al.* (1994) in defining mean size of seals in any age class as the size at the end of the breeding season each year. For seals less than 1 year old this means from the time that they are weaned from their mothers and are nutritionally independent. For juveniles it is equivalent to their mass at the beginning of the moult haulout.

To determine growth rates of females I used the nose tail lengths of the above females that were aged from teeth and juveniles that had been immobilised for stomach flushing (Slip 1995, Slip and Woods 1996), and fitted these to a Gompertz growth model using least squares nonlinear regression (Fig. 7.1). I determined the relationship between nose-tail length and mass to be  $\text{mass (kg)} = 293.05 * \text{length (m)} - 343.08$ , and used this to estimate mean mass at the end of the breeding season. As only limited data are available for males I used the lengths and masses calculated for elephant seals at South Georgia and Macquarie Island (Boyd *et al.* 1994, Australian Antarctic Division, unpublished data), and modified these to fit masses obtained from adult males at Heard Island.

#### 7.2.1.3 Biomass of Seals

Pup production for the Heard Island population in 1992 was approximately 17000 (This volume, Chapter 3). Assuming a sex ratio at birth of 1:1, and a stable population age structure the number of individuals in the population was about 72,000 including weaned pups (This volume, Chapter 3). The biomass of each age class was derived from the product



**Fig. 7.1:** The relationship between nose-tail and age in years for female southern elephant seals at Heard Island. The line represents a Gompertz growth model fitted by least squares regression. The regression equation was:  $\text{Nose-tail length} = 2.541 * e^{(-0.625 * \exp(-0.492 * \text{age}))}$ ,  $r^2 = 0.854$ .

of the number of individuals in an age class and their mean mass (Table 7.1). The biomass of each age class was determined from the product of the mean mass of individuals in each age class by the number of individuals in that age class.

Total biomass was converted to total body gross energy (TBGE) using the equation of Reilly and Fedak (1990) derived from body composition analysis of grey seals. I assumed mean total body water (TBW) to be 52% for adult males and adult females, and 60% for juveniles derived from estimates using tritium dilution technique (Slip *et al.* 1992a, Boyd *et al.* 1993, M. A. Hindell and M. Lea pers. comm.).

### 7.2.2 Energy Expenditure

The annual cycle of southern elephant seals involves two terrestrial phases and two marine phases, and can be summarized into four distinct activities: foraging at sea, moult, reproduction in adult seals, and mid year haulouts in juvenile seals and some adults (this volume, Chapter 3). Each of these activities have an associated energetic cost that varies depending on the age, sex, and reproductive status of the seal. In addition, energy will be required for growth, which varies with age. Total energy expenditure for an individual seal can be expressed as:

$$E_T = E_F + E_R + E_G + E_M + E_H$$

where

$E_T$  = total energy expenditure

$E_F$  = energy costs of foraging including travel to and from foraging area

$E_M$  = energy costs of moult

$E_R$  = energy costs of reproduction

$E_G$  = energy costs of growth

$E_H$  = energy cost of haulout not associated with reproduction or moult

#### 7.2.2.1 Energy Cost of Foraging

The energy costs of foraging includes the assimilation efficiency, the heat increment of digestion, the heat increment of locomotion, and the time spent foraging. There are no



**Table 7.1:** Population parameters used to estimate the energy requirements of southern elephant seals at Heard Island. Survival rates for females were calculated from age structure at Heard Island. Survival rates for males were modified from McCann's (1985) life tables for South Georgia.

Age	Females				Males			
	Survival Rate ( $l_x$ )	STL (m)	Girth (m)	Mass (kg)	Survival Rate ( $l_x$ )	STL (m)	Girth (m)	Mass (kg)
0	1.000	1.44	1.41	114	1.000	1.45	1.42	117
1	0.613	1.74	1.40	171	0.600	1.80	1.44	176
2	0.476	2.01	1.56	237	0.510	2.05	1.60	271
3	0.422	2.20	1.66	271	0.422	2.26	2.00	486
4	0.367	2.33	1.78	288	0.350	2.98	2.51	771
5	0.349	2.41	1.83	301	0.290	3.33	2.84	1086
6	0.257	2.46	1.89	332	0.241	3.65	3.12	1402
7	0.239	2.49	1.91	355	0.193	3.82	3.31	1652
8	0.220	2.51	1.94	383	0.145	3.95	3.44	1892
9	0.147	2.52	1.96	400	0.101	4.04	3.51	1971
20	0.128	2.53	1.98	418	0.071	4.10	3.55	2017
11	0.092	2.53	2.00	433	0.050	4.15	3.60	2068
12	0.073	2.53	2.05	471	0.035	4.25	3.63	2117
13	0.055	2.54	2.05	474	0.024	4.35	3.65	2158
14	0.037	2.54	2.05	474	0.017	4.40	3.65	2179
15	0.018	2.54	2.05	474	0.012	4.45	3.65	2192
16	0.013	2.54	2.05	474	0.008	4.48	3.67	2207
17	0.009	2.54	2.05	474	0.005	4.48	3.67	2207
18	0.007	2.54	2.05	474	0.003	4.48	3.67	2207
19	0.006	2.54	2.05	474	0.002	4.48	3.67	2207
20	0.004	2.54	2.05	474	0.001	4.48	3.67	2207
21	0.002	2.54	2.05	474				
22	0.001	2.54	2.05	474				

values available for assimilation efficiency or for the heat increment of digestion for southern elephant seals. However, assimilation efficiency in other pinnipeds is high and varies between 90% and 94% of gross energy intake (Keiver *et al.* 1984, Prime and Hammond 1987, Fisher *et al.* 1989, Fadely *et al.* 1990). The heat increment of digestion was estimated to be 17% of gross energy intake for harp seals (Gallivan and Ronald 1981). I have assumed 92% assimilation efficiency, and 17% for the heat increment of digestion to determine the energetic cost of foraging.

The work required to transport a body through seawater is given by:

$$E = 0.5 * r * CD * A * V^2 * L, \quad (\text{Williams 1987, Boyd } et al. 1994)$$

where            E = work (joules)  
                     r = average water density ( $1.027 \times 10^3 \text{ kg/m}^3$  for the Southern Ocean)  
                     CD = the coefficient of drag, assumed to be 0.12 (Boyd *et al.* 1994)  
                     A = the maximum cross-sectional area of the body ( $\text{m}^2$ )  
                     V = velocity (m/sec)  
                     L = distance (m).

The maximum cross sectional area was determined from the average girths of animals in each age class given in Table 7.1. The girths for females were obtained from seals that had been aged from teeth, and the girths for 1 to 3 year old males were determined from animals measured at Heard Island. The girths of older males were estimated from age distributions from South Georgia (Boyd *et al.* 1994), and Macquarie Island (Slip unpublished data), with the maximum girths determined from measurements of breeding adult males from Heard Island.

I estimated average velocity by taking the average daily horizontal transit velocity of seals tracked from Heard Island and calculated the additional vertical component to velocity for two shapes of dives. The first assumed a V shaped dive of average depth and average

surface interval, and the second assumed a symmetrical dive of average depth, average bottom time and average surface interval (Table 7.2). These estimates were 1.2 and 1.5 m/s. These estimates only take in the vertical and horizontal component of the dive (which would increase the estimates) or the use of currents or eddies (which would decrease the estimates). These estimates were similar to the 1.3 m/s reported by Le Boeuf *et al.* (1992) for a northern elephant seal but less than the 2.1 m/s recorded for a southern elephant seal for the first 3 weeks on leaving Macquarie Island (Hindell and Lea 1997). As this latter measurement is during the time of greatest rate of travel, I have assumed an average swim velocity over the whole period at sea of 1.4 m/s. Swimming efficiency, power output as a percentage of power input, varies with velocity and was recorded at about 10% at 1.4 m/s in harbour seals (Williams *et al.* 1991).

Southern elephant seals spend on average 88% of total time at sea under water, diving almost continuously. There are two types of dive where seals may not be working to move through the water but may be conserving energy. These are the processing type 3 dives (Slip 1997), where for part of the dive the seals either sink passively or float towards the surface depending on their relative buoyancy (Crocker *et al.* 1997), and the type 2 benthic foraging dives (Slip *et al.* 1994), where the profile of the dive is flat at the bottom. I have assumed that seals were not actively swimming during the flat profile phase of the dive, and hence incurring no energetic cost. Processing dives accounted for 5% of total time at sea for all age classes and the non-active phase of these dives accounted for about 60% of the dive. Type 2 benthic dives did not occur in juvenile seals from Heard Island (Slip 1997), but these dives accounted for 3% of time at sea for adult females from Heard Island, and 34% of time at sea for adult males from Heard Island, and the non active bottom phase of the dive accounted for an average of 52% of the dive (Slip, unpublished data). Type 2 benthic dives were absent from juveniles (Slip 1997), and rare in adult females (3% of time at sea), but common in adult males constituting 34% of time at sea (unpublished data).

**Table 7.2:** Distance travelled, mean dive parameters, and two approximations of swimming speed for southern elephant seals from Heard Island. Velocity 1 is the rate of movement required to travel at the observed surface rate assuming dives are V-shaped of average depth, duration, and surface interval. Velocity 2 is the rate of movement required to travel at the observed surface rate assuming dives are of average depth and duration, and have average bottom time (defined as time spent at depths greater than 85% of the maximum depth of the dive), and surface interval.

Seal	Sex	Mean Surface Speed		Mean Dive Parameters				Estimated Swimming Speed	
		Km day <sup>-1</sup>	m sec <sup>-1</sup>	Max. Depth (m)	Duration (min)	Surface time (min)	Bottom time (min)	Velocity 1 (m sec <sup>-1</sup> )	Velocity 2 (m sec <sup>-1</sup> )
91-1602	PMF	101	1.17	422	25.5	2	11.6	1.27	1.52
91-1603	PMF	89	1.03	326	28.8	2	13.7	1.08	1.24
91-1604	PMF			405	29.5	2	14.9		
91-1605	PMF	91	1.06	433	26.9	2	14.0	1.17	1.28
91-1607	PMF	76	0.88	437	29.3	2	14.7	1.00	1.13
90-1114	PMF	84	0.98	326	21.8	2	10.8	1.08	1.24
89-802	PMF	97	1.13	450	29.7	2	13.7	1.22	1.43
89-807	PMF	88	1.02	438	27.5	2	12.2	1.13	1.37
93-1504	PBF	115	1.33	341	17.2	3	6.3	1.45	1.99
93-1505	PBF	95	1.09	468	18.2	3	7.8	1.32	1.70
93-707	PBF	157	1.81	355	19.2	2	8.6	1.90	2.29
89-1119	PBF	103	1.19	193	14.0	3	5.8	1.25	1.66
89-1120	PBF	90	1.04	324	18.6	2	9.4	1.17	1.34
87-706	PMM	86	1.00	305	39.7	2	23.2	1.02	0.94
87-707	PMM			470	26.8	3	12.9		
89-810	PMM	90	1.04	497	30.0	4	16.1	1.15	1.28
92-1504	PMM	88	1.02	557	28.0	9	12.8	1.13	1.50
92-1505	PMM	132	1.53	224	25.9	5	9.7	1.57	2.30
<b>Mean ± SE PMF</b>		<b>89 ± 3</b>	<b>1.04 ± 0.04</b>	<b>405 ± 18</b>	<b>27.4 ± 0.9</b>	<b>2.0 ± 0.1</b>	<b>13.0 ± 0.5</b>	<b>1.1 ± 0.1</b>	<b>1.3 ± 0.1</b>
<b>Mean ± SE PBF</b>		<b>112 ± 12</b>	<b>1.29 ± 0.14</b>	<b>337 ± 44</b>	<b>17.5 ± 0.9</b>	<b>2.5 ± 0.3</b>	<b>7.6 ± 0.7</b>	<b>1.4 ± 0.1</b>	<b>1.8 ± 0.2</b>
<b>Mean ± SE PMM</b>		<b>99 ± 11</b>	<b>1.15 ± 0.13</b>	<b>411 ± 63</b>	<b>30.1 ± 2.5</b>	<b>5.1 ± 1.3</b>	<b>14.9 ± 2.3</b>	<b>1.2 ± 0.1</b>	<b>1.53 ± 0.3</b>
<b>Mean ± SE</b>		<b>99 ± 5</b>	<b>1.15 ± 0.06</b>	<b>388 ± 24</b>	<b>25.4 ± 1.5</b>	<b>3.0 ± 0.5</b>	<b>12.1 ± 1.0</b>	<b>1.2 ± 0.1</b>	<b>1.5 ± 0.1</b>

Average time at sea was determined by subtracting known average time ashore for various age groups. In their first year seals were at sea for 310 days and ashore for a post weaning fast of about 47 days (Arnbom *et al.* 1993), and a mid winter haulout of about 9 days duration (unpublished data). Two year olds and three year olds year seals were at sea for 320 days, adult females for 310 days and adult males for 265 days. At Heard Island, adult females are ashore for 26 days during the breeding season (this volume, Chapter 3), and 28 days during the moult, while adult males are ashore for about 60 days during the breeding season and about 40 days for the moult (unpublished data).

#### 7.2.2.2 *Spatial Component of Foraging*

To determine the amount of food that the Heard Island population takes from the Kerguelen Plateau I assumed that the location data from geolocation tracked animals (this volume, Chapter 5, Slip 1997) was representative of the population. From these data I assumed that juvenile seals of 2 years and less spent 60% of days at sea on the Kerguelen Plateau, adult females and subadult males spent 30% of time at sea there (assuming the post moult period at sea accounted 76.6% of total time at sea), and adult males spent 29% of time at sea there.

#### 7.2.2.3 *Energy Cost of Reproduction*

Total energy expenditure for female southern elephant seals during lactation, which includes metabolic rate and the energy of milk production, has been reported as  $3222 \pm 161$  MJ at South Georgia (Fedak *et al.* 1994) and  $3228 \pm 440$  MJ at Macquarie Island (Hindell and Slip 1997). These are very similar even though the length of lactation was 23 days for South Georgia and 24 days for Macquarie Island. The lactation period at Heard Island was 21.5 days (Slip 1997), and as there are no measurements of energy expenditure during lactation at Heard Island I have used a total energy expenditure of 3200 MJ which converts to an average daily energy expenditure of 148.8 MJ/day. This represents 6.5 times the predicted standard metabolic rate (SMR) where  $SMR = 0.293 W^{0.75}$  MJ/day (Lavigne *et al.* 1986).

Thus, the energy of reproduction for an individual female was obtained from  $6.5 \times \text{SMR} \times 21.5 \text{ MJ}$ .

The mean mass of southern elephant seal pups at birth was 37 kg (Slip 1997). The energy density of foetal seals at term has not been calculated for southern elephant seals. The proportion of body mass represented by fat in newborn southern elephant seal pups at Macquarie Island was 3.8% (Hindell *et al.* 1994b). The hydration of lean body mass in seal pups is generally higher than adults, and has been measured at 74.7% in Antarctic fur seal pups (Arnould *et al.* 1996), 73.8% in harp seal pups (Worthy and Lavigne 1983, Iverson *et al.* 1993), and 73.6% in ringed seals (Lydersen *et al.* 1992). As there are no data available for southern elephant seals I have assumed hydration of lean body mass to be 74%. Using standard values for the energy density of fat and protein as 39.5 MJ/kg and 23.5 MJ/kg respectively (Schmidt-Nielsen 1983), the energy density of elephant seal pups at term was 7.6 MJ/kg. The mass of southern elephant seal placentas was 5 kg (Boyd *et al.* 1994), and I assumed an energy density of 0.46 MJ/kg (Lavigne and Stewart 1979) to calculate total energy content.

There is little information about the energetic cost of reproduction of male southern elephant seals. Boyd *et al.* (1994) used a metabolic rate of 3.3 times SMR based on measurements of northern elephant seals and Antarctic fur seals (Deutch *et al.* 1990, Boyd and Duck 1991). I have used this figure to calculate the costs of reproduction in males greater than 6 years. Adult bulls were ashore at Heard Island during the breeding season from late August to late November (Slip 1997). I have assumed an average tenure to be 60 days. Weaned pups were resighted from between 30 and 52 days after weaning, and the average duration of the post weaning fast was 46 days (Slip unpublished data).

#### 7.2.2.4 Energy Cost of Moul

The energy cost of moul in southern elephant seals was estimated to be 2.4 times SMR for adult females (Boyd *et al.* 1993), and 1.7 times SMR for adult males (Slip *et al.*

1992b). The moult lasts on average 28 days for adult females and 40 days for adult males (Ling and Bryden 1981).

#### 7.2.2.5 *Energy Cost of Growth*

I calculated the annual growth increment from the data on body mass and converted this to energy using the equation of Reilly and Fedak (1990) for total body gross energy to convert this increment to energy. Although the body composition of southern elephant seals changed over different stages of the life cycle, these changes are relatively small so I assumed that growth of body components was proportional to growth in total mass (see Boyd *et al.* 1994).

#### 7.2.2.6 *Energy Cost of Haulout Other than Reproduction or Moulting*

Juvenile elephant seals return to their natal islands and haulout in winter (this volume, Chapter 3). Also, adult males and females occasionally haul out on sea ice during their winter foraging trips but these were between 2 and 30 hours, and the average total time spent hauled out during foraging trips was 23 hours (Slip, unpublished data). I have assumed males over 6 years and females over 4 years haul out for 1 day during foraging. Juveniles from Macquarie Island haul out an average of 9 days in winter (Antarctic Division, unpublished data), and I have assumed females 2 years and under and males 5 years and under haul out for 9 days, while 6 year old males haul out for 5 days and 4 year old females for 2 days. As animals behaved similarly during the winter haulout as they did during the moult, but without the metabolic requirement for moulting skin, I have calculated the metabolic requirements of the haulout ( $E_H$  MJ) for the duration of  $D_H$  days, from the equation:

$$E_H = 1.5 \times \text{SMR} \times D_H .$$

### 7.2.3 Diet Composition and Energy Consumption

It has been difficult to obtain a quantitative measure of the diet of the southern elephant seal because it is not possible to sample from animals at their main feeding grounds and because of differential digestion rates of their main prey. The only information available on the diet comes from stomach samples obtained at haulout sites. Laws (1956) examined 139 stomachs from South Georgia 108 of which were empty, and found 26 contained squid, nine contained fish, and only six contained fresh remains, of which five contained fish and one contained squid. Thus, he suggested that the diet of elephant seals consisted of 75% squid and 25% fish by weight (Laws 1977). Recent studies of the diet of southern elephant seals (eg. Green and Burton 1993, Slip 1995) have noted the difficulty of quantifying the relative importance of fish and squid in the diet due to differential digestion of squid beaks and fish otoliths. However, if the relative proportion of squid and fish in the diet is calculated using the same presence/absence method used by Laws, then at Heard Island the proportions are 55% squid to 45% fish (Slip 1995). Although fish may still be under represented from stomach flushed samples due to their rapid rate of digestion, these proportions were based on hard remains such as fish eye lenses, fish bones, and squid beaks. I assumed that diet measured by stomach lavaging was indicative of overall diet.

Energy densities vary among species of squid, and as values were unavailable for most species in the diet, I divided the squid diet into muscular squid, gelatinous squid, and cranchiid squid which have a leathery mantle following Boyd *et al.* (1994). I determined the relative importance by mass of each species in the diet of adult males, adult females, and juvenile elephant seals from Slip (1995), and Green and Burton (1993). I assigned energy densities of squid from Clarke *et al.* (1985) (Table 7.3).

Energy densities for nototheniids are in the range of 4.5 - 6.1 MJ/kg, for channichthyids in the range of 5.2 - 5.8 MJ/kg (G. Robertson, Australian Antarctic Division, unpublished data), and for myctophids in the range of 7.0 to 8.0 MJ/kg (Cherel and Ridoux



**Table 7.3:** Cephalopods in the diet of southern elephant seals from Heard Island.

Proportions of squid species were taken from Slip (1995), and energy densities were taken from Clarke *et al.* (1985).

Squid Species	% Total Squid Biomass in diet			Squid Type	Energy Density (MJ/kg)
	Juvenile	Adults			
		Male	Female		
<i>Allureoteuthis antarcticus</i>	0.7	6.8	11.5	muscular	4.0
<i>Brachioteuthis</i> sp.	0.0	0.0	0.1	muscular	4.0
<i>Chroteuthis</i> sp.	0.0	0.02	0.2	gelatinous	2.0
<i>Galiteuthis glacialis</i>	0.0	1.2	0.7	cranchiid	1.7
<i>Gonatus antarcticus</i>	3.0	3.1	3.1	muscular	4.0
<i>Histioteuthis eltaninae</i>	0.2	0.0	0.2	gelatinous	2.0
<i>Kondakovia longimana</i>	2.6	71.8	39.6	cranchiid	1.7
<i>Liocranchia</i> sp.	0.0	0.0	<0.1	cranchiid	1.7
<i>Martialia hyadesi</i>	57.1	0.0	0.8	muscular	4.0
<i>Mastigoteuthis</i> sp. B	0.0	0.0	<0.1	gelatinous	2.0
<i>Mastigoteuthis</i> sp.?	2.2	0.4	0.5	gelatinous	2.0
<i>Moroteuthis ingens</i>	0.9	0.0	15.9	muscular	4.0
<i>Moroteuthis knipovitchi</i>	7.0	9.5	21.9	muscular	4.0
<i>Psychroteuthis glacialis</i>	0.4	7.1	5.4	muscular	4.0
<i>Taonius pavo</i>	0.0	0.0	<0.1	cranchiid	1.7
<i>Todarodes filippovae</i>	25.9	0.0		muscular	4.0

1992). I assumed that the fish taken by elephant seals was a mixture of myctophids, nototheniids and channichthyids. The relative importance of fish species was determined from Green and Burton (1993), and Slip (1995) (Table 7.4). The unidentified myctophid and channichthyid were considered to be size equivalents of *Electrona antarctica*, and *Channichthys rhinoceratus*, respectively.

The total biomass of each item in the diet was calculated from the gross energy requirement (GE) of the population so that:

$$GE = P_{1,m} P_{1,e} + P_{2,m} P_{2,e} + P_{3,m} P_{3,e} + \dots + P_{n,m} P_{n,e}$$

where  $P_{1,m}$ ,  $P_{2,m}$ , ...,  $P_{n,m}$  denote the total mass consumed of each prey item, and  $P_{1,e}$ ,  $P_{2,e}$ , ...,  $P_{n,e}$  denote the energy value of each prey item expressed as MJ/kg. The proportions by mass of each item in the diet was used to solve this equation such that:

$$P_{n,m} = GE / (R_1 P_{1,e} + R_2 P_{2,e} + R_3 P_{3,e} + \dots + R_n P_{n,e})$$

where  $R_1$ ,  $R_2$ , ...,  $R_n$  are the ratios of  $P_{n,m}$  to the mass of the other items in the diet.

As it was not possible from stomach flushing studies to determine the relative importance of squid and fish in the diet with any confidence I have presented the estimate of biomass consumed assuming the composition of diet to be 55% squid to 45% fish following Green and Burton (1993) and Slip (1995). To demonstrate how changes in diet composition affects estimates of consumption, I have also presented estimates of consumption assuming 75% squid to 25 % fish following Laws(1977) as a possible composition.

## 7.3 RESULTS

### 7.3.1 Energy Requirements of the Population

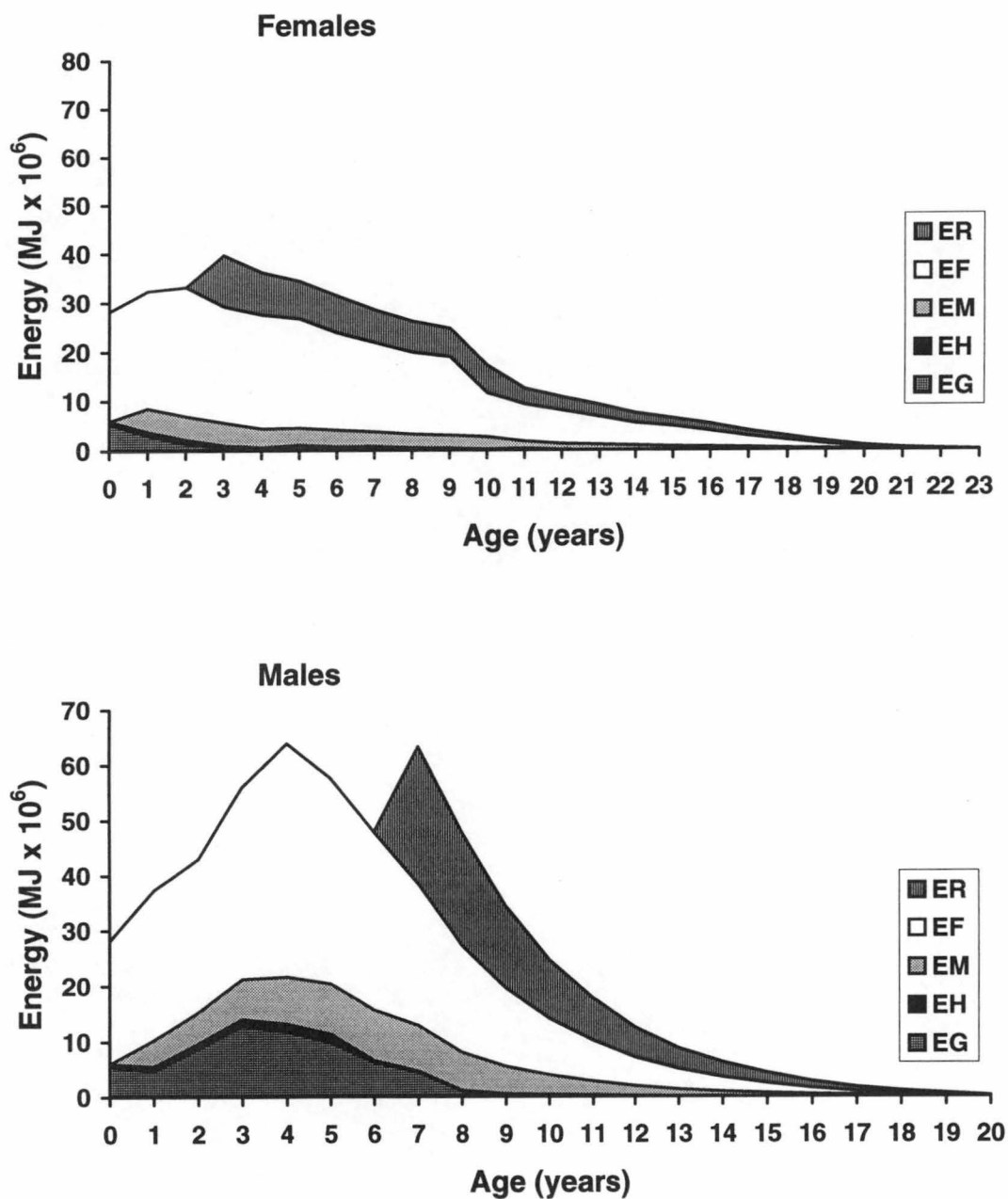
The total population size was 72,000, with a sex ratio of 1.13 females to each male. This represented a total biomass of 33,000 tonnes with 69% represented by male biomass.

**Table 7.4:** Fish species in the diet of southern elephant seals from Heard Island. Proportions of fish species by mass were taken from Green and Burton (1993) and Slip (1995), and energy densities were taken from Cherel and Ridoux (1992) and G. Robertson (Australian Antarctic Division, unpublished data).

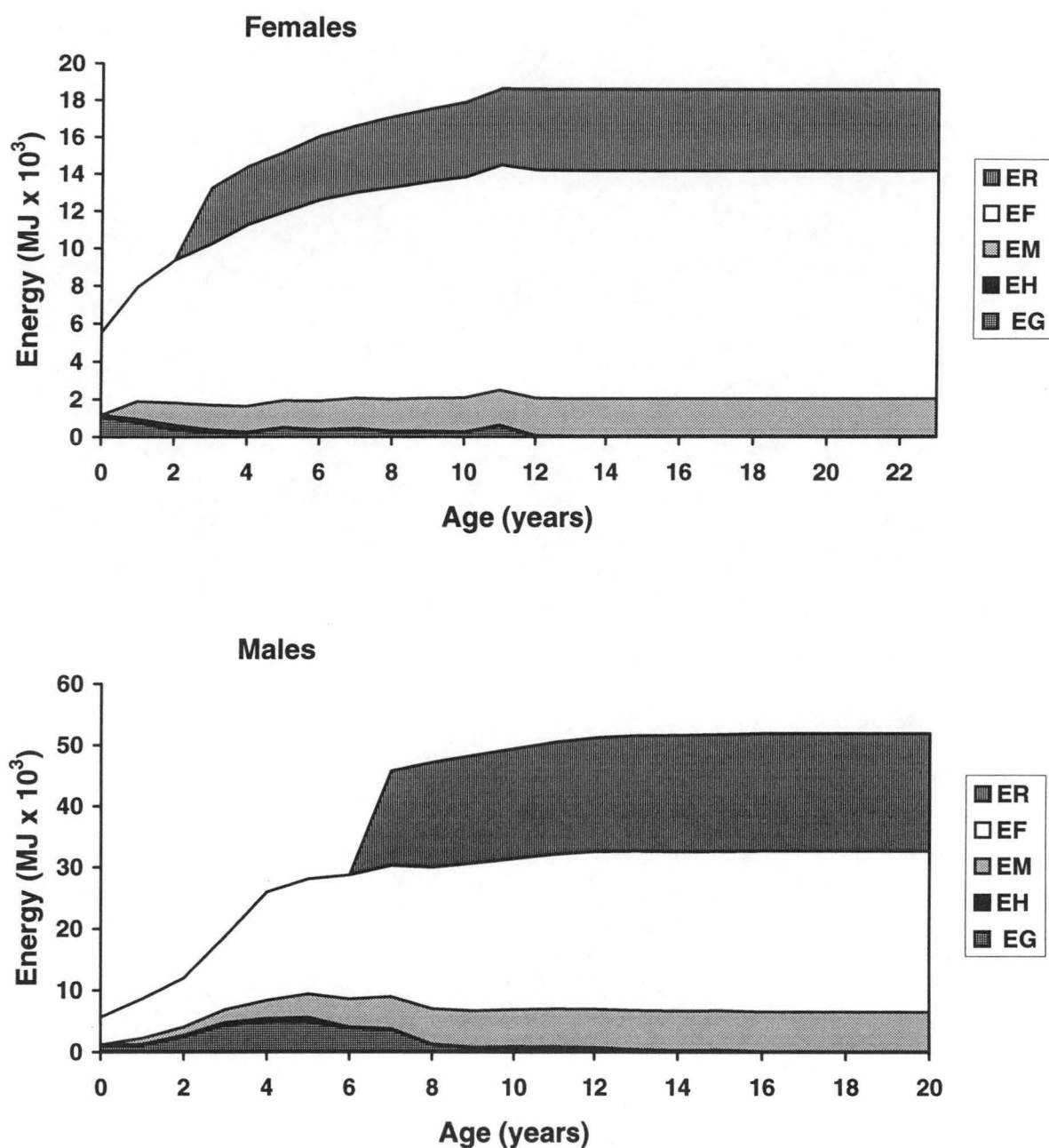
% Total Fish Biomass in Diet					
Fish Species	Juvenile	Adults		Family	Energy Density MJ kg <sup>-1</sup>
		Male	Female		
<i>Electrona antarctica</i>	92.1	0.9	4.4	Myctophidae	7.5
<i>Electrona carlsbergi</i>	7.9	0.8	8.1	Myctophidae	7.5
<i>Gymnoscopelus braueri</i>		0.1		Myctophidae	7.5
<i>Gymnoscopelus nicholsi</i>		0.6	2.1	Myctophidae	7.5
Unidentified myctophid		0.8	1.5	Myctophidae	7.5
<i>Dissostichus eleginoides</i>		83.6	59.2	Nototheniidae	5
<i>Notothenia squamifrons</i>		3.9	7.4	Nototheniidae	5
<i>Notothenia acuta</i>		2.3	4.4	Nototheniidae	5
<i>Nototheniops mizops</i>		1.4	2.2	Nototheniidae	5
<i>Channichthys rhinoceratus</i>		2.0	3.7	Channichthyidae	5.5
<i>Champsocephalus gunnari</i>		1.0	2.0	Channichthyidae	5.5
Unidentified channichthyid		2.6	4.9	Channichthyidae	5.5

The average body mass of seals was 676 kg and 263 kg for males and females respectively, while the average body mass of seals 3 years or older was 913 kg and 347 kg for males and females respectively. The estimated total annual assimilated energy for the Heard Island population was  $9.53 \times 10^8$  MJ, or  $13.2 \times 10^3$  MJ per seal. The total energy consumption of the population changed with age reflecting changes in size, numbers, and reproductive condition (Fig. 7.2). Energy expenditure associated with foraging was 56.2% and 65.3% of total annual energy costs for males and females respectively. Reproduction was the next largest energy demand and represented 17.0% and 19.3% of total annual energy costs for males and females respectively. Energy expended on the moult represented 13.6% and 0.9% of total annual energy costs for males and females respectively. Energy expended on growth was 11.9% and 3.8% of total annual energy costs for males and females respectively, while energy expended on haulouts other than for reproduction and moult contributed 1.3% and 1.0% of total annual energy costs for males and females respectively. The energy requirements for individual seals increased gradually until the onset of reproductive activity which caused a steep increase in energy expenditure at age 3 and 4 years in females and age 7 years in males (Fig. 7.3).

The total annual gross energy requirements of the Heard Island population was  $1.24 \times 10^9$  MJ, or  $17.2 \times 10^3$  MJ *per capita*. Males used 59% of the energy required by the population. The production efficiency, or the proportion of assimilated food energy deposited as body mass was 8.4%. While at sea gross energy intake during potential foraging time was on average 76.2 MJ /seal/day for males, and 42.1 MJ /seal/day for females. This varied with size such that juveniles consumed 30-40 MJ/day, adult females consumed 65-80 MJ /day, and adult males consumed 150 to 250 MJ /day. Based on average dive rates (Table 7.2), this converts to an average capture rate of about 0.2 kg, 0.5 kg, and 1.8 kg of muscular squid and fish per dive, for juveniles, adult females and adult males respectively.



**Fig. 7.2:** Changes in energy expenditure of different age classes for males and females of the population of southern elephant seals at Heard Island. ER = energy required for reproduction, EF = energy required for foraging, EM = energy required for moult, EH = energy required for haulouts not associated with reproduction or moult, EG = energy required for growth.



**Fig. 7.3:** Per capita energy expenditure of different age classes of the southern elephant seal population at Heard Island. ER = energy required for reproduction, EF = energy required for foraging, EM = energy required for moult, EH = energy required for haulouts not associated with reproduction or moult, EG = energy required for growth.

### 7.3.2 Food Consumption

The total biomass of squid and fish consumed (assuming 55% squid) annually by the population of elephant seals at Heard Island was 311 thousand tonnes. Of this juveniles consumed 49.8 thousand tonnes, subadult males consumed 57.2 thousand tonnes, adult females consumed 97.6 thousand tonnes, and adult males consumed 106.4 thousand tonnes (Table 7.5). The relative biomass of the species consumed suggested that seals concentrated on the higher energy prey species such as myctophids, and the muscular squid species. While in the region of the Kerguelen Plateau seals consumed an estimated 106.6 thousand tonnes or about 34% of prey, including 23.8 thousand tonnes of *Dissostichus eleginoides* (Table 7.6).

## 7.4 DISCUSSION

As with most models of pinniped energy requirements it is difficult to put statistical confidence limits on estimates of energy expenditure and of food consumption as the quality of data are variable (e.g. Lavigne *et al.* 1985, Boyd *et al.* 1994). Because of this the absolute figures for energy expenditure and food consumption should be treated with some caution. However, it is worth considering how variation among the different parameters of the model affect the subsequent estimates. As the energetic cost of foraging was by far the largest contributor to total energy cost, changes to this estimation will have the most profound effect on the estimates of energy expenditure and food consumption. The most sensitive parameter appears to be swim speed, and distance travelled. For example, a change in mean swim speed of  $0.1 \text{ m sec}^{-1}$  results in a change in energetic cost and in food consumption of about 10%. This highlights the importance of examining at sea behaviour in order to increase the confidence of the estimates of consumption.

Other parameters had less effect on the outcome of estimates for consumption. For example, changes in the mass of each age class had only a small effect and a change in mass of adult seals of 50 kg resulted in a change in consumption of about 1.5%. Changing the initial estimate of total population size was directly reflected in the estimate for consumption.

**Table 7.5:** Expected biomass of various food items consumed by different age classes of the southern elephant seal population from Heard Island, given different compositions by mass of squid to fish in the diet. Juveniles were defined as 2 years and under, subadult males were 3 to 5 year olds, adult females were at least 3 years , and adult males were at least 6 years.

Total Biomass Consumed (x 10 <sup>3</sup> tonnes)								
Percentage of Squid in Diet	Juveniles		Subadult Males		Adult Female		Adult Male	
	55%	75%	55%	75%	55%	75%	55%	75%
<b>Fish Prey</b>								
<i>Electrona antarctica</i>	20.1	12.7	1.14	0.72	1.95	1.22	0.44	0.29
<i>Electrona carlsbergi</i>	1.72	1.09	2.09	1.31	3.57	2.24	0.38	0.25
<i>Gymnoscopelus braueri</i>							0.01	0.01
<i>Gymnoscopelus nicholsi</i>			0.53	0.33	0.91	0.57	0.30	0.20
Unidentified myctophid			0.38	0.24	0.65	0.41	0.38	0.25
<i>Dissostichus eleginoides</i>			15.2	9.56	26.0	16.3	40.0	26.4
<i>Notothenia squamifrons</i>			1.90	1.19	3.25	2.04	1.88	1.24
<i>Notothenia acuta</i>			1.14	0.71	1.94	1.22	1.12	0.74
<i>Nototheniops mizops</i>			0.57	0.36	0.97	0.61	0.66	0.43
<i>Channichthys rhinoceros</i>			0.96	0.60	1.64	1.03	0.95	0.62
<i>Champscephalus gunnari</i>			0.51	0.32	0.87	0.54	0.50	0.33
Unidentified channichthyid			1.27	0.80	2.16	1.36	1.25	0.82
<b>Squid Prey</b>								
<i>Alluroteuthis antarcticus</i>	0.19	0.29	3.61	5.57	6.17	9.51	3.98	6.44
<i>Brachioteuthis</i> sp.			0.03	0.05	0.05	0.08		
<i>Chiroteuthis</i> sp.			0.06	0.10	0.11	0.17	0.01	0.02
<i>Galiteuthis glacialis</i>			0.22	0.34	0.38	0.58	0.70	1.14
<i>Gonatus antarcticus</i>	0.80	1.24	0.97	1.50	1.66	2.56	1.81	2.93
<i>Histioteuthis eltaninae</i>	0.53	0.83	0.06	0.10	0.11	0.17		
<i>Kondakovia longimana</i>	0.69	1.07	12.4	19.2	21.2	32.8	42.0	68.0
<i>Liocranchia</i> sp.			0.03	0.05	0.05	0.08		
<i>Martialia hyadesi</i>	15.2	23.61	0.25	0.39	0.43	0.66		
<i>Mastigoteuthis</i> sp. B			0.03	0.05	0.05	0.08		
<i>Mastigoteuthis</i> sp.?	0.59	0.91	0.16	0.24	0.27	0.41	0.23	0.38
<i>Moroteuthis ingens</i>	0.24	0.37	4.99	7.70	8.53	13.15		
<i>Moroteuthis knipovitchi</i>	1.86	2.89	6.88	10.6	11.7	18.11	5.56	8.99
<i>Psychroteuthis glacialis</i>	1.06	1.65	1.70	2.62	2.90	4.47	4.16	6.72
<i>Taonius pavo</i>			0.03	0.05	0.05	0.08		
<i>Todarodes filippovae</i>	6.89	10.71						
<b>Total</b>	<b>49.8</b>		<b>57.2</b>		<b>97.6</b>		<b>106.4</b>	



**Table 7.6:** Estimated total biomass consumed by southern elephant seals from Heard Island and estimated biomass taken from the Kerguelen Plateau assuming the proportion of squid to fish in the diet 55% and 75% by mass. Most consumed items for the 55% squid diet are highlighted in bold.

Percentage of Squid in Diet	Total Biomass ( x 10 <sup>3</sup> tonnes)		Biomass taken from Kerguelen Plateau ( x 10 <sup>3</sup> tonnes)	
	55% squid	75% squid	55% squid	75% squid
<b>Fish Prey</b>				
<i>Electrona antarctica</i>	<b>23.6</b>	14.9	<b>13.1</b>	8.27
<i>Electrona carlsbergi</i>	<b>7.76</b>	4.89	<b>2.8</b>	1.78
<i>Gymnoscopelus braueri</i>	0.01	0.01	0.004	0.002
<i>Gymnoscopelus nicholsi</i>	1.74	1.10	0.51	0.33
Unidentified myctophid	1.41	0.89	0.41	0.26
<i>Dissostichus eleginoides</i>	<b>81.2</b>	52.3	<b>23.8</b>	15.3
<i>Notothenia squamifrons</i>	<b>7.02</b>	4.47	<b>2.07</b>	1.32
<i>Notothenia acuta</i>	4.20	2.67	1.24	0.79
<i>Nototheniops mizops</i>	2.20	1.40	0.65	0.41
<i>Channichthys rhinoceratus</i>	3.54	2.25	1.04	0.66
<i>Champscephalus gunnari</i>	1.87	1.19	0.55	0.35
Unidentified channichthyid	4.68	2.98	1.38	0.88
<b>Squid Prey</b>				
<i>Alluroteuthis antarcticus</i>	<b>13.9</b>	21.8	<b>4.16</b>	6.51
<i>Brachioteuthis</i> sp.	0.09	0.13	0.03	0.04
<i>Chiroteuthis</i> sp.	0.18	0.28	0.05	0.08
<i>Galiteuthis glacialis</i>	1.30	2.05	0.38	0.60
<i>Gonatus antarcticus</i>	<b>5.25</b>	8.24	1.79	2.80
<i>Histioteuthis eltaninae</i>	0.70	1.09	0.37	0.57
<i>Kondakovia longimana</i>	<b>76.4</b>	121.0	<b>22.6</b>	35.7
<i>Liocranchia</i> sp.	0.09	0.13	0.03	0.04
<i>Martialia hyadesi</i>	<b>15.9</b>	24.7	<b>9.32</b>	14.5
<i>Mastigoteuthis</i> sp. B	0.09	0.13	0.03	0.04
<i>Mastigoteuthis</i> sp.?	1.25	1.94	0.55	0.85
<i>Moroteuthis ingens</i>	<b>13.8</b>	21.2	<b>4.15</b>	6.40
<i>Moroteuthis knipovitchi</i>	<b>26.0</b>	40.6	<b>8.25</b>	12.9
<i>Psychroteuthis glacialis</i>	<b>9.81</b>	15.5	<b>3.20</b>	5.04
<i>Taonius pavo</i>	0.09	0.13	0.03	0.04
<i>Todarodes filippovae</i>	<b>6.89</b>	10.7	<b>4.14</b>	6.42
<b>total squid biomass</b>	<b>171.74</b>	269.59	<b>59.04</b>	92.52
<b>total fish biomass</b>	<b>139.23</b>	89.06	<b>47.57</b>	30.37
<b>total biomass</b>	<b>310.97</b>	358.64	<b>106.60</b>	122.89

This was not unexpected because in a population with a stable age structure, food consumption is proportional to population size. However, a change in any of the individual population parameters will result in a change in the age structure, and therefore the *per capita* consumption of the population (Hiby and Harwood 1985). As survival decreases, the average energy requirement of the population decreases, though only slowly, while a decrease in fecundity or growth rate can result in a considerable *per capita* increase in energy requirements, which is largely due to changes in the age and mass structure of the population (Hiby and Harwood 1985). In general, a knowledge of changes in the population size is not sufficient for reliable predictions about changes in food consumption because changes in the age structure will alter food consumption.

A major deficiency in the model and in current knowledge of elephant seal foraging ecology is the relative importance of fish and squid in the diet. I have assumed the composition of squid in the diet to be 55% based on presence/absence data (see Chapter 4, this volume), but fish could be either more or less important in the diet by mass. The results show that changing the percentage of squid in the diet from 55 to 75% changes the estimates of consumption for individual prey species quite dramatically (Tables 7.5 and 7.6).

Another major assumption of the model is that the composition of prey from stomach flushing animals ashore reflects the diet of the seals when they are at their distant foraging grounds. Experiments on captive animals have shown that southern elephant seals digest food very quickly with a rate of passage of about 9 hours (Krockenberger and Bryden 1994). These authors suggested that the short retention times may only apply to captive animals as diving would probably cause a reduction in gut movements, and the long intestine may act as a storage-digestion compartment for when the animal is submerged. However, movement of food out of the stomach would occur relatively quickly in free diving animals. How long difficult to digest parts such as squid beaks and fish eye lenses remain in the stomach is unknown although McConnell and Fedak (1996) assumed that stomach flushed samples

represented feeding from about 2-3 days. While the composition of prey species used here may be a good reflection of what seals take from the Kerguelen Plateau, it is probably not representative of food taken from near the Antarctic continental shelf. Some prey that were commonly taken by elephant seals are unknown from Antarctic waters, but similar species not recorded in the diet do occur there (see Chapter 5, this volume).

The parameters that have the most influence on the estimates of food consumption were the energy densities of prey species. The energy densities of squid have been estimated from northern hemisphere species, while the energy densities of some fish species have been estimated from closely related species. Further, the energy density of prey species consumed may change with location and with season (Lavigne *et al.* 1982). Thus, energy densities may vary from the estimates in the model, and this could have a substantial effect on the estimates of consumption for particular prey. For example, if the energy value of *Dissostichus eleginoides* is increased from 5 to 7.5 MJ kg<sup>-1</sup> then the estimated consumption from the Kerguelen Plateau drops from 23.8 thousand tonnes to 19.7 thousand tonnes. If the energy density of *Kondakovia longimana* was changed from 1.7 to 3 MJ kg<sup>-1</sup> then the estimate of its consumption changes from 22.6 thousand tonnes to 17.1 thousand tonnes and the estimate for *D. eleginoides* drops further to 18.1 thousand tonnes or about 76% of the original estimate. While changes in the energy densities of the prey species that were most important by mass, changes in the energy density of minor prey in the diet has little effect on the estimates of consumption for the more commonly consumed items.

While the absolute amounts of energy requirements and particularly food consumption should be treated with caution, comparisons with similar studies based on energy consumption support the accuracy of the results. The *per capita* energy requirements for southern elephant seals from Heard Island was 17.2 x 10<sup>3</sup> MJ year<sup>-1</sup>, while Boyd *et al.* (1994) estimated the *per capita* energy requirements of southern elephant seals from South Georgia at 16.8 x 10<sup>3</sup> MJ year<sup>-1</sup>, and Lavigne *et al.* (1985) estimated a *per capita* energy

requirement of  $11.3 \times 10^3$  MJ/year for the much smaller harp seals (adult harp seals weigh about 135 kg - King 1983).

Another method of checking the validity of energy expenditure is to examine average metabolic rate for the population over the year and examine how this might influence diving performance. Assuming that seals dive at or close to their theoretical aerobic dive limit (TADL) most of the time (Slip *et al.* 1994), then it is possible to determine how long seals would be able to dive aerobically while consuming oxygen at the rate suggested by the population metabolic rate. While on the surface heart rate was about 3.4 times submerged heart rate in an adult female southern elephant seal (Hindell and Lea 1997), and assuming heart rate is proportional to metabolic rate in elephant seals as has been reported for California sea lions *Zalophus californianus* (Butler *et al.* 1992), then the population energy expenditure can be broken into that portion consumed while diving, and that consumed while on the surface. The estimate of gross energy requirements for the Heard Island population was about 1.75 times the standard metabolic rate averaged over one year. As seals spend 90% of time underwater then metabolic rate while diving would be 1.41 times SMR. The average energy expenditure for males three years and over in the population was 2.52 ml O<sub>2</sub>/minute/kilogram while for females three years and over it was 3.44 ml O<sub>2</sub>/minute/kilogram. The figure for females compares well with the 3.64 ml O<sub>2</sub>/minute/kilogram estimated by Hindell and Lea (1997) based on heart rate data for an adult female during the first 50 days at sea following the breeding season. The available oxygen stores for elephant seals have been calculated at 86.2 ml O<sub>2</sub>/minute/kilogram (Kooyman 1989), which means that males and females could dive aerobically for on average 31.8 minutes and 25.0 minutes respectively. The recorded mean dive duration for adult male elephant seals from Heard Island was 30.1 minutes while the mean duration for post breeding adult females was 17.44 minutes and for post moult adult females was 27.4 minutes. The annual mean dive duration for adult females taking into account the proportion of time spent at sea during each of these foraging trips was

25.1 minutes. These estimates of mean dive duration are close to the population estimates of the TADL, which is further evidence supporting the accuracy of the estimation of energy consumption.

With the exception of Boyd *et al.* (1994), most models of elephant seal food consumption have been based on crude estimates of biomass that have been scaled by a factor to estimate annual consumption. Laws (1977) suggested annual food intake could be estimated by biomass multiplied by 20. Several subsequent estimates of consumption continued to use this method (e.g. Condry 1981, McCann 1985, Woehler and Green 1992). Boyd *et al.* (1994) suggested that the multiplier should be around 10, which was similar to the estimate for Harp seals suggested by Lavigne *et al.* (1986). The present study suggests that the multiplier was closer to 9 and it is possible that further refinement of the model may lower this number further. There are several ways in which elephant seals might conserve energy, and one is that there may be seasonal changes in metabolic rate. In captive harp seals seasonal fluctuations in metabolic rate caused animals to gain weight more rapidly even though they ate less food, and the implications of this were that if wild seals consumed at similar rates they would consume considerably less food than was previously estimated by bioenergetic models (Renouf *et al.* 1993). In addition, information on the diving behaviour, including swim speed and heart rate data have suggested that elephant seals have several physiological adaptations to enable them to conserve energy (Hindell and Lea 1997).

My estimate of food consumption of 311 thousand tonnes was considerably higher than the estimate made by Woehler and Green (1992) as part of a larger estimate of consumption of marine resources by the Heard Island community of seabirds and seals. These authors estimated consumption by southern elephant seals to be 45.8 thousand tonnes, but this was based on only a portion of the breeding population and consumption was estimated using a crude estimate of food consumed per unit biomass. However, when my model of energy expenditure and food consumption was applied to the section of the

population considered by Woehler and Green (1992), then this portion of the population consumed 21.6 thousand tonnes of food annually. Alternatively, the method used by these authors produced an estimate of annual consumption of 660 thousand tonnes when applied to the whole population.

The estimate for the amount of prey consumed by elephant seals from the Kerguelen Plateau considers only the Heard Island breeding population. It seems likely that the population that breeds on Îles Kerguelen also feed extensively on the Kerguelen Plateau as adult males tagged there have been resighted in the Vestfold Hills, along with adult males that had been tagged at Heard Island (Burton 1985, Bester 1988b, Guinet *et al.* 1992). The Heard Island and the Îles Kerguelen populations represent about 30% and 68% respectively of the Kerguelen stock. However, the amount of foraging overlap between these populations is unknown.

The estimate for consumption by elephant seals of the commercially targeted *D. eleginoides* from the Kerguelen Plateau was 23,800 tonne. The total abundance of *D. eleginoides* in a 200 nautical mile zone around Heard Island was estimated from trawl surveys at 17,700 tonnes in 1990, 3,200 tonnes in 1992, and 11,900 tonnes in 1993 (Williams and de la Mare 1995), while estimates for the area around Îles Kerguelen were 105,000 tonnes in 1987 and 45,000 tonnes in 1988 (Duhamel 1988). These figures suggest that the estimates for consumption may be high and/or the estimates of abundance may be low, given that elephant seals consumed fish up to 650 mm in length (Slip 1995), and the maximum recorded length was 2150 mm (Fischer and Hureau 1985). However, the estimates for abundance do not include the part of the population in water greater than 800 m (Williams and de la Mare 1995), and fish at these depths would be well within the range of elephant seal diving as over 10% of dives by adult males were below 800 m (this volume, Chapter 5). In addition, Antarctic fur seals consume *D. eleginoides* (Green *et al.* 1989). The estimate of consumption of *C. gunnari* by elephant seals on the Kerguelen Plateau (1,870 tonnes) was

much less than the estimates of abundance (3112 to 31701 tonnes) in the Heard Island zone (Williams and de la Mare 1995).

This model suggests that commercial fisheries on the Kerguelen Plateau may compete with southern elephant seals for *D. eleginoides*. However, as the southern elephant seal consumes a broad range of prey, what effect this competition might have on the population remains uncertain. The magnitude of population change in the Kerguelen stock populations over the last 40 years highlights the importance of regularly monitoring these populations in conjunction with fishing activities.

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## CHAPTER 8

### CONCLUSIONS

This study has emphasised the importance of the southern elephant seal as a major consumer of squid and fish in the Southern Ocean ecosystem.

While the population at Heard Island declined by about 50% between 1949 and 1985, there has been little change from 1985 to 1992. In 1992 total pup production at Heard Island was between 17,000 and 18,000, which converts to a total population of between 72,300 and 76,500 seals at the end of the breeding season, including pups of the year. Thus, the population at Heard Island represents 9% of the world population of southern elephant seals or 30% of the Kerguelen stock group. While a number of hypotheses have been proposed to explain the decline of all elephant seal populations in the Kerguelen and Macquarie stocks, environmental change that resulted in a reduction in sea ice and hence primary productivity in the Southern Ocean seems the most likely explanation. These populations had recovered from the effects of nineteenth century commercial sealing and may have been food limited by the 1960's, while the population at South Georgia which has been stable since 1950 was still being harvested and may not have been limited by food availability.

Analyses of stomach contents from animals at Heard Island showed that muscular squid and fish were the main prey of the southern elephant seal. Because elephant seals digest food quickly, dietary studies based on stomach contents are somewhat limited. Also, as seals digest squid and fish at different rates, it is difficult to determine the relative importance of squid and fish. However, the presence of fish remains in the diet suggested that fish may be more important than the 75% squid to 25% fish that has become enshrined in the literature. Frequency of occurrence of fish and squid suggested this ratio might be 55% squid to 45% fish. The presence in the diet of the Patagonian tooth fish (*Dissostichus eleginoides*), which is commercially harvested on the Kerguelen Plateau, suggested that there



is potential for commercial fishing to impact on the southern elephant seal population at Heard Island.

Elephant seals from Heard Island can travel several thousand kilometres away from the island during their at-sea migrations. Movements followed a pattern of periods of relatively fast movement, particularly when leaving Heard Island, punctuated by periods where activity was concentrated in a relatively small area. Most activity occurred south of the Antarctic Polar Front (97.7% of seal days at sea), and the main areas used by seals were the Kerguelen Plateau, the Antarctic continental shelf region, and pelagic regions south of the APF. Most activity occurred between 200 and 800 m depth although over 10% of adult male dives were greater than 800 m. There was a distinct diurnal pattern in dive depth with shallower dives occurring at night, and when seals were located in areas where a steep thermocline existed, then shallower night time dives often occurred close to the thermocline.

Juveniles seals tended to dive slightly less deeply than adults, and had slightly shorter dive durations, although it appeared that by the end of their first year some seals would be capable of dives to about the same depths as adults. The edge of the Kerguelen Plateau and the Antarctic Polar Frontal Zone appeared to be the most important foraging areas for juvenile seals in this study.

The Heard Island elephant seal population had an annual gross energy requirement of  $1.24 \times 10^9$  MJ, or  $17.2 \times 10^3$  MJ *per capita*, and the energetic costs of foraging, including travel to and from foraging areas, contributed most to this. The population consumed 311 thousand tonnes of fish and squid annually of which 97.7% was taken from south of the Antarctic Polar Front and 34% was taken from the area over the Kerguelen Plateau. Included in the estimate of consumption from the Kerguelen Plateau was 23.8 thousand tonnes of the commercial species *Dissostichus eleginoides*.

To give the population estimate of food consumption in Chapter 7 a global perspective I have estimated consumption for the other populations of southern elephant seals. Assuming that the other populations have similar energetic requirements to the Heard Island population, and that dietary composition consists of 55% squid to 45% fish, then food consumption can be estimated by multiplying biomass by 9.4. Using the population estimates given in Table 1.1 (corrected by their respective population trends to give an estimate of population size in 1996), McCann's (1985) age distributions for South Georgia, Patagonia/Falklands and Macquarie stocks, and the age distributions in chapter 7 for the Kerguelen stock populations, total annual consumption would be 2.35 million tonnes for the South Georgia stock, 289 thousand tonnes for the Patagonia/Falklands stock, 453 thousand tonnes for the Macquarie stock, and 1.20 million tonnes for the Kerguelen stock. Thus, total annual consumption for all populations of southern elephant seals is estimated at 4.3 million tonnes. In addition, about 70% of this food would be taken from Antarctic waters as elephant seals from the South Georgia population spend about 23% of time north of the Antarctic Polar Front (McConnell and Fedak 1996), seals from Patagonia spend 100% of time north of the APF (Campagna *et al.* 1995), seals from Macquarie Island spend about 30% of time north of the APF (Antarctic Division, unpublished data). There are no data available on the foraging areas of elephant seals from Îles Kerguelen but it is located on the APF, and the limited data from Marion Island (Bester and Pansegrouw 1992), and tag resight data (Bester 1988b, Guinet *et al.* 1992) suggest that this population probably spends about 30% of time north of the APF. Thus, the global population of elephant seals consumes about 3.05 million tonnes of fish and squid from waters south of the APF, and 1.24 million tonnes of squid and fish from sub-Antarctic waters to the north of the APF.

While a bioenergetic model of southern elephant seal populations integrates what is known about the southern elephant seal, it also highlights areas where information is lacking. The areas where more information might refine the estimates of consumption include

metabolic performance at sea, swim speed over the entire year, dietary composition by mass, and information on the energy densities of the major prey species. By far the greatest gap in our understanding of the foraging ecology of the southern elephant seal is what they eat when they are at their distant foraging grounds. In order to fill this gap it seems likely that novel methods will be required. For example, methods that integrate diet over a long period such as stable isotope analysis or fatty acid profiles may prove useful in helping to solve this problem. Also, sophisticated remote sensing and recording devices may become available in the future that enable the recording of feeding events while the seals are at sea.

While this study has provided many insights into the behaviour of the elephant seal population at Heard Island it is limited in that it only covers a single year. How the movement patterns change from year to year with changes in the distribution and abundance of prey remains unclear. Examining the behaviour of the predators and their prey in concert may prove to be a fruitful area for future work.

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