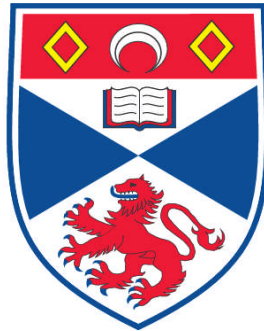


**ESTIMATING THE DISTRIBUTION OF DEMAND FOR  
ANTARCTIC KRILL (EUPHAUISA SUPERBA) FROM LAND-  
BASED PREDATORS AT SOUTH GEORGIA**

**Matthew Lewis Swarbrick**

**A Thesis Submitted for the Degree of PhD  
at the  
University of St. Andrews**



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# **Estimating the distribution of demand for Antarctic krill (*Euphausia superba*) from land-based predators at South Georgia**

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A thesis submitted in accordance with the regulations of the University of St

Andrews for the degree of

**Doctor of Philosophy**

by

**Matthew L. Swarbrick (BSc honours)**

February 2006

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## AUTHORS DECLARATION

I, Matthew L Swarbrick, hereby certify that this thesis, which is approximately 52000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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## Acknowledgments

For as long as I remember I have dreamt of wildlife filled and wave swept lonely islands. Little did I think they would lead me to one of the most wildlife filled and wave swept of them all, South Georgia, and to what could have been a lonely pursuit, a PhD. It is to those who prevented it from been lonely and made it a joyful challenge that I owe thanks.

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## Abstract

South Georgia is renowned for the abundance of Antarctic krill (*Euphausia superba*) and a range of krill predators. Variability in krill availability at a range of scales, and the consequences of this for predator-prey interactions, mean that quantifying the spatially explicit demand for krill by those predators is essential to understanding the mechanisms underlying ecosystem changes in the region. In this thesis demand within a distinct study box to the northwest of the island has been assessed. The thesis has three sections; (1) the number of predators; (2) the distribution of predators; and (3) the demand for krill by those predators.

- (1) Predator densities with confidence intervals were determined from appropriately designed shipboard transect survey; counts of Antarctic fur seals (*Arctocephalus gazella*), macaroni penguins (*Eudyptes chrysolophus*), gentoo penguins (*Pygoscelis papua*), and Antarctic prions (*Pachyptila desolata*) were adjusted for sea state, distance from observer and dive behaviour. Providing the first at-sea predator density estimates for the region.
- (2) A comparison of the distribution of female Antarctic fur seals engaged in pup-rearing (using satellite telemetry) and the whole population that were not restricted to a single part of the population (from shipboard transect survey) was undertaken. Using two general additive models based on the relationship between seal distribution (one derived from transect and the other from telemetry) and the physical environment indicated that the spatial distribution of lactating females is representative of the general population.
- (3) Using the derived predator density, the local krill demand estimate was 2581 tonnes krill per day, a consumption rate of 0.45% per day of the concurrently estimated krill biomass (using shipboard acoustics). Antarctic fur seals accounted for 75% of this demand. This level of demand was less than the increase in biomass resulting from krill growth. However, based on the length-specific demand, determined from concurrent predator diet samples demand exceeded growth for krill >48mm.





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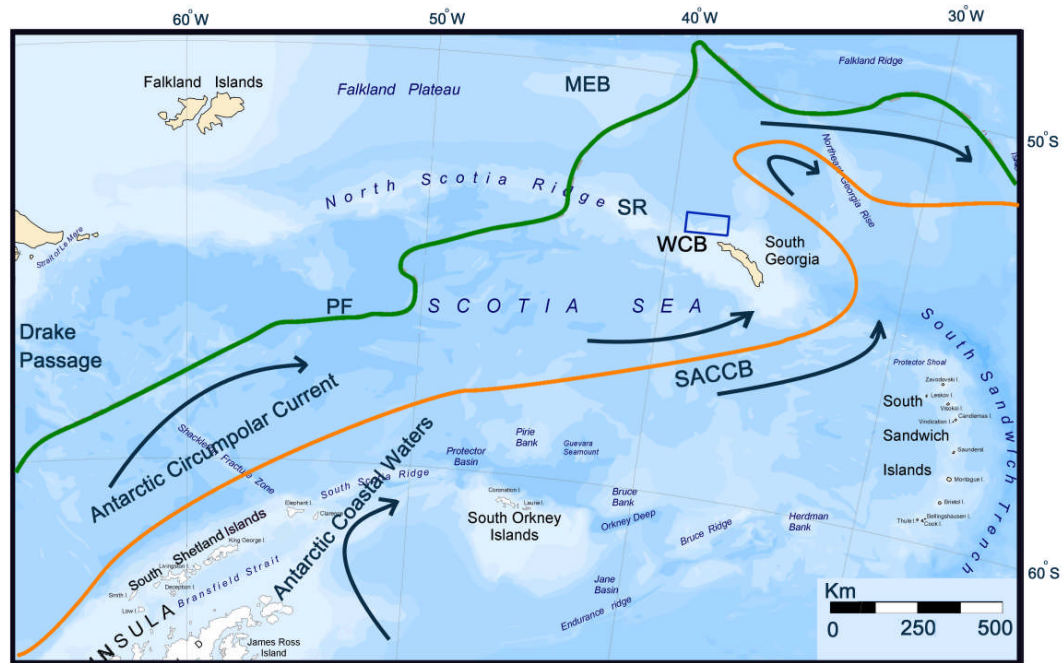
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## CHAPTER ONE

### General introduction

#### 1.1 Introduction

South Georgia is an oceanic island lying in the Southwest Atlantic to the south of the Antarctic Polar Frontal Zone (APFZ), and within the Southern Ocean water mass (Figure 1.1). The waters surrounding South Georgia are unusually productive (Brandon et al. 1999; Constable et al. 2003) with the values of zooplankton biomass around the island roughly four to five times higher than those typical of the Southern Ocean as a whole (Atkinson et al. 2001). Being an isolated island surrounded by highly productive waters the island is host to large populations of land-breeding marine predators (Croxall and Prince 1979). Many of these predators rely principally upon Antarctic krill (*Euphausia superba*), hereinafter called krill, for food (Doidge and Croxall 1985; Croxall and Lishman 1987; Croxall et al. 1997).



**Figure 1.1.** Map showing the Scotia Sea region, South Georgia and the Western Core Box (WCB) study area. Also shown are the major oceanographic features of the region; Polar front (PF), Antarctic Circumpolar Current, Southern Antarctic Circumpolar Boundary (SACCB) and the Antarctic Coastal Waters (after Orsi et al. (1995) and Trathan et al. (1997)) as well as areas of distinct bathymetry, the Maurice Ewing Bank (MEB) and Shag Rocks (SR).

The high biomass of krill, fish and air-breathing predators in the region has attracted commercial interests since the 17<sup>th</sup> Century, and the island has a long history of exploitation (Headland 1984). Harvesting began with the taking of Antarctic fur seals (*Arctocephalus gazella*) in the 18<sup>th</sup> and 19<sup>th</sup> centuries (Bonner 1968). This was followed by exploitation of the great whales and elephant seals (*Mirounga leonina*) in the mid 20<sup>th</sup> century (Harmer 1931; Mackintosh 1965; Headland 1984) and then in turn, various fish species (Everson 1992). Alongside current finfish fisheries, there is also now a fishery for krill. Though the current total catches for the Southern Ocean are small (130000–150000 tonnes per annum) compared with the total allowable catch of 4.3 million tonnes (Constable et al. 2000), the fishery is expected to increase in the future (Everson et al. 2000; Nicol and Foster 2003; Croxall and Nicol 2004; Hewitt et al. 2004b).

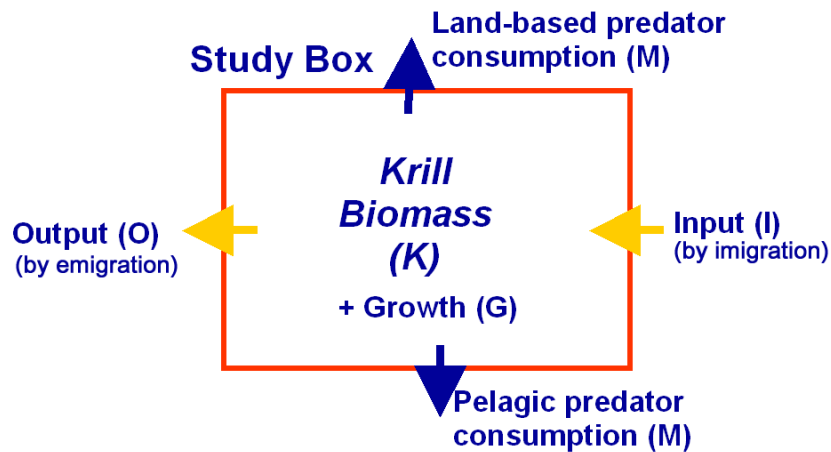
Present catch levels are not a threat to krill stocks. However, at South Georgia the fishery overlaps with many species that may already be in competition for krill; such competition is likely to be localised, especially for species that have to feed land-based young that depend on krill (Barlow et al. 2002). In order to ensure that fishing does not compete with predators, precautionary catch limits have been agreed that take into account the needs of predators (Hewitt et al. 2004b). Though often considered as an exemplar of the ecosystem-based method of management, these catch limits are still based upon incomplete knowledge about the energetic requirements of predator populations and the availability of krill. The local availability of krill varies from year to year (Brierley et al. 1997; Murphy et al. 1998; Trathan et al. 2003), and years of particularly low abundance can have a pronounced negative effect on the reproductive success of some krill consuming species (Croxall et al. 1999; Reid 2002; Forcada et al. 2005; Reid and Forcada 2005; Trathan et al. 2006). Different krill predators show varying levels of reproductive success in different years when krill may not be equally available to each predator species (McCafferty et al. 1998b; Croxall et al. 1999; Barlow et al. 2002).

Accompanying the levels of commercial exploitation, the region also has a long history of dedicated scientific research. Studies began with the *Discovery Investigations* of the 1920's (Kemp and Bennet 1932; Hardy and Gunther 1935), and continue to the present day. Most of this recent research work has been conducted by the British Antarctic Survey. The *Discovery Investigations* were ahead of their time, in that they took an ecosystems approach (Atkinson et al. 2001; Garcia et al. 2003). They set out to

understand the causes of the high primary productivity, and how this was linked with whale fisheries. An ecosystem-based approach is now applied to fisheries management, and is coordinated through the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) (Everson 1995; Agnew 1997; Hewitt and Linen Low 2000; Constable 2004).

A fundamental aspect of this ecosystem-based approach is understanding the spatial and quantitative relationships between the predators within the ecosystem and their prey (Cairns 1987; Monaghan 1996; Agnew 1997; Trathan et al. 2001). Knowledge is now increasingly available about predator diet (Reid and Arnould 1995; Reid et al. 1996; Reid et al. 1997b), the overall demand for krill (Boyd 2002a; Hewitt et al. 2004c), individual behaviour (Barlow and Croxall 2002b; Boyd et al. 2002; Staniland and Boyd 2003) and of the krill standing stock (Trathan et al. 1995; Hewitt et al. 2004a).

To meet their energetic demand, predators have specific requirements for krill at certain patch densities, at certain depths in the water column and of sufficient energetic value. There is therefore a need to be able to quantify the localised demand for krill by predators and to be able to balance this with the krill available to them. Quantifying this demand gives a value for a key variable in the krill flux equation (Figure 1.2), the solving of which was a key part of the British Antarctic Surveys DYNAMOE programme (Dynamics and Management of Ocean Ecosystems).



**Figure 1.2. Functional diagram of the key processes involved in the krill flux balance.**

The marine ecosystem in the Southern Ocean has long been typified as a simple food chain with phytoplankton, krill and higher predators (Knox 1970). Though this description is relatively simplistic (Clarke 1985), it still holds true and, at least in the Scotia Sea, krill are the major link in the transfer of energy from primary producers to larger organisms (Murphy et al. 1988). The unique trophic structure, combined with the region's high productivity, high plankton and predator concentrations (Atkinson et al. 2001), makes the region an excellent model for investigating the links between regional marine ecosystems and large-scale biological and physical processes (Trathan and Murphy 1998; Trathan et al. 2003; Weimerskirch et al. 2003; Forcada et al. 2005; Reid et al. 2005; Trathan et al. 2006) and for developing ecosystem-based fisheries management (Constable 2002; Constable 2004);

## **1.2 Background information**

To help place this thesis in context it is useful to review the background knowledge of the ecosystem and the study animals:

### ***1.2.1 Antarctic krill and the Southern Ocean***

The total krill biomass in the Southern Ocean has been estimated by different studies at between 25 million tonnes and 1900 million tonnes, with the stock representing 10 to 50% of Southern Ocean zooplankton biomass (Knox 1994). The most likely estimates, based on consumption by predators, or acoustic survey methods, put estimates at 200 – 400 million tonnes (Miller and Hampton 1989) see also Trathan et al. (1995) and Hewitt et al. (2004b).

Although the distribution of krill is circumpolar, it is far from uniform (Fogg 1998; Siegel 2005). Studies of oceanography and zooplankton in the Scotia Sea region have identified South Georgia as having high krill biomass. Local conditions favour fast planktonic growth rates and local oceanography potentially leads to high retention of the krill within the system (Murphy et al. 1998; Murphy et al. 2004).

South Georgia sits in a zone of mixing, the Weddell Scotia Confluence (WSC), between two easterly flowing water masses (Hardy and Gunther 1935; Trathan et al. 1997; Brandon et al. 2004; Murphy et al. 2004) (Figure 1.1). The first is the Antarctic Circumpolar Current (ACC), a current which forms a ring in the northern part of the Southern Ocean between the Polar Front (PF) and the Southern Antarctic Circumpolar Boundary (SACCB) (Orsi et al. 1995). This current carries water from the Bellingshausen Sea through the Drake Passage into the region of South Georgia. The second water mass, Antarctic Coastal Water, comes from closer to the continent, along the Antarctic Peninsula and from the Weddell Sea (Priddle et al. 1988). Modelling studies have found it likely that this confluence carries krill to South Georgia from the regions of high krill production along the northern

Antarctic Peninsula (Hoffman et al. 1998; Lascara et al. 1999), although these studies have also noted that this is highly variable, not least because of the variability in the flow and position of the fronts of the ACC (Brandon et al. 2004).

The easterly flow of the ACC upon reaching the Scotia Arc and South Georgia, are deflected northwards, forcing the PF to lie 250-300 km to the north of South Georgia (Trathan et al. 1997). The Southern Antarctic Circumpolar Current (SACC) curves around the northern edge of the South Georgia shelf break, causing the water to flow anticyclonically westwards (Trathan et al. 1997; Atkinson et al. 2001). Where this reversed SACC flow meets the westerly flowing ACC, to the north and west of South Georgia there is a substantial mixing zone (Orsi et al. 1995; Brandon et al. 1999; Atkinson et al. 2001; Brandon et al. 2004). These high levels of mixing, combined with local high nutrient enrichment, from both the seabed and from island run-off give South Georgia high planktonic growth rates (Atkinson et al. 2001).

Over the shelf, the mixing of local waters with the oceanic circulating waters and localised gyres reduce the rate of physical transport (Meredith et al. 2005). This results in higher residence times and retention of plankton in the system, in turn making the plankton potentially more available to predators.

Long term records show that the most reliable place to find krill at South Georgia is the shelf break to the north and central region of the island (Kemp and Bennett 1932; Hardy and Gunther 1935; Trathan et al. 2003), and this area is now one of the main focuses of the winter krill fishery (Trathan et al. 1998a). However, krill is much more widely distributed, and studies



attempting to find associations between their distribution and temperature, primary productivity, oxygen concentration and salinity have not come to clear conclusions (Murphy et al. 1991; Goss and Everson 1996). Trathan et al. (2003) found fine-scale relationships between krill density and bathymetry; that indicated that the shelf break region, and waters over the shelf, particularly between 250 and 750 m, have consistently higher biomass than deeper waters.

### ***Krill variability***

There is considerable inter-annual variability in zooplankton composition and density at South Georgia. In some years this has resulted in an almost complete absence of krill (Priddle et al. 1988; Brierley et al. 1997; Trathan et al. 2003). One reason for this may be variability in the recruitment within the source populations along the northern Antarctic Peninsula (Brierley et al. 1999). Variability in these populations may result from variations in sea ice extent and interactions with other zooplankton (Loeb et al. 1997). There also seems to be variability in the advection of krill to South Georgia dependent on large-scale physical forcing of the two water masses influencing the position of the WSC (Hofmann and Murphy 2004; Murphy et al. 2004). South Georgia is downstream of large-scale temperature and sea ice anomalies in the Southern Pacific (White and Peterson 1996), which may be connected to El Niño Southern Ocean (ENSO) events (Gloersen 1995; Trathan and Murphy 2002). These may then influence sea-surface temperature at South Georgia, though how this links with krill variability is not yet understood (Trathan et al. 2003).

Fluctuations in krill populations have great influence on the breeding success of dependent predator populations (Boyd and Murray 2001; Reid and Croxall 2001; Reid and Forcada 2005). Whilst it is clear that there is a relationship between the abundance of krill and the success of its predators (Reid et al. 1999a; Reid et al. 1999c), the temporal and spatial scales of this relationship are less clear. It is therefore essential to understand the spatial distributions and scales of the interactions between predators and krill populations.

### ***1.2.2 Krill predators***

Krill are eaten by birds, including albatrosses, petrels, prions and penguins (Croxall and Lishman 1987; Croxall et al. 1997), demersal (Kock et al. 1992) and pelagic fish (Kock 1987), squid (Nicol and Odor 1985; Kock 1987; Daneri et al. 1999), baleen whales (Nemoto 1966; Laws 1985; Ribic et al. 1991; Kawamura 1994; Mori and Butterworth 2004) and some species of seals, of which there are three that are considered to be dependent upon krill. Of these, the crabeater seal (*Lobodon carcinophagus*), and the leopard seal (*Hydrurga leptonyx*) occupy the fast ice and pack ice zones (Bester et al. 2002). The crabeater seal is abundant and is thought to comprise half the world's total stock of seals; its diet is over 95% krill. The leopard seal's diet is over 30% krill (Walker et al. 1998; Hall-Aspland et al. 2005). The third species of seal is the Antarctic fur seal, which inhabits the sub-Antarctic Islands. In this introduction I review the two most important species, respectively the most important marine mammal the Antarctic fur seal and the most important seabird the macaroni penguin, *Eudyptes chrysolophus*.

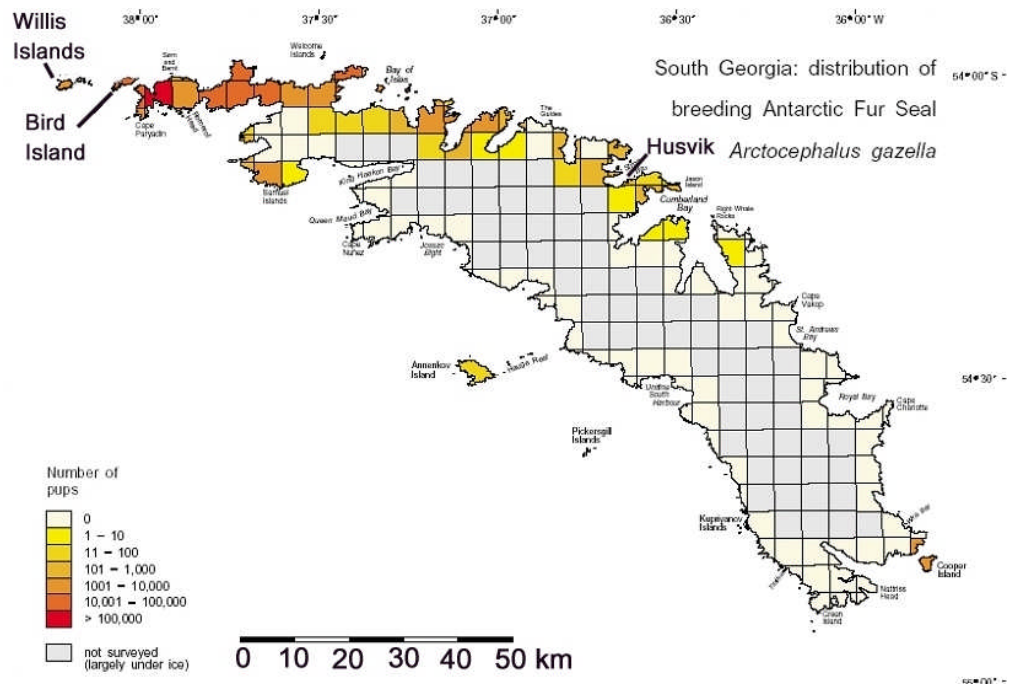
### ***1.2.3 The Antarctic fur seal***

#### ***Distribution***

The Antarctic fur seal occurs predominantly south of the PF, and approximately 96% of the world population breeds at South Georgia (Boyd 1993). Smaller populations also occur on the more southerly islands in the Scotia Sea, principally the South Shetland, South Orkney and South Sandwich Islands, as well as along the northwest coast of the Antarctic Peninsula. Before sealing these were favoured breeding grounds. In recent years larger breeding colonies have returned though these more southerly populations still mainly consist of non-breeding animals. (Jablonski et al. 1987; Bengston et al. 1990; Huckle-Gaete et al. 2004). The species also occurs in smaller numbers at Bouvetøya (Kirkman et al. 2000), Marion Island and Prince Edward Island (Kerley 1983), Kerguelen (Bester and Roux 1986), Macquarie Island (Shaughnessy and Fletcher 1987) and Heard Islands (Shaughnessy and Goldsworthy 1990) in the South Atlantic and Indian Oceans.

The fur seal population at South Georgia is closely linked to those at the other islands in the Scotia Sea, and there is movement of individuals between them (Boyd et al. 1998). Recent tagging of both male and female seals outside the breeding season has shown that males migrate from the breeding grounds at South Georgia to the South Orkney Islands and other islands in the Scotia Sea. Though many females remained in the South Georgia region, some also travelled north to the Patagonian Shelf (Boyd et al. 1998). Though breeding takes place around much of the South Georgia coastline, the larger colonies are situated at the northwestern end of the island

and on Bird Island (Boyd 1993; Trathan et al. 1996b) ( $54^{\circ} 00'S$ ,  $38^{\circ} 02'W$ ), indicated on Figure 1.3.



**Figure 1.3.** The distribution of Antarctic fur seal breeding colonies around South Georgia. Sourced from Trathan et al. (1996b).

### *Diet*

Studies of lactating females during the breeding season at South Georgia found krill to occur in 88% of scats, with fish occurring in 47% and squid in 5%, these results are based on a four year average (Reid and Arnould 1995). Fur seal diet composition very much reflects local availability (Croxall and Pilcher 1984; Doidge and Croxall 1985; Kirkman et al. 2000). In periods of low krill availability, a greater proportion of the diet is comprised of fish and squid. This same pattern is reflected in the length and maturity composition of the krill taken. Though seals show a preference for krill over a certain length, and also for sexually active females, their diet still reflects the length-frequency distribution of the available krill population (Murphy and Reid 2001).

Fish composition in the diet has been found to be mainly the myctophid *Protomyctophum choridon* (98% of fish biomass consumed) between early February and the middle of March. Outside of this period *Champscephalus gunnari* and *Lepidonotus larseni* agg., have been found to make up 94% of the total biomass of fish consumed (North et al. 1983; Reid and Arnould 1995; North 1996). Many of the fish taken are epipelagic and are associated with krill swarms, it may be that these are not targeted but are taken opportunistically by the seals (North 1996).

The diet of male fur seals is similar to that of females in that it is made up predominantly of krill, but fish make up a greater proportion of the diet (Reid 1995; North 1996; Casaux et al. 2003). Bonner and Hunter (1982) also noted that sub-adult males have been observed to kill and eat macaroni penguins and giant petrels.

### ***Breeding ecology***

Fur seals come ashore to breed, generally at large, well-established breeding colonies. The first males arrive to establish territories in early November (Duck 1990). The adult females come ashore in early to mid December seeming to prefer the presence of other females (Bonner and Laws 1964). Younger males (less than 5 years old) are not usually able to establish territories of their own, and tend to occupy the margins of the breeding area or shallow water (Bonner and Laws 1964). Harems start to break up in mid-January, and males then tend to disperse from the breeding grounds (Duck 1990; Boyd et al. 1998).

Females give birth shortly after they arrive at the breeding beach, often within 24 hours and begin suckling the pups immediately. The female

comes into oestrus around six to eight days later and copulation then takes place (Duck 1990). The pup will then be left on the beach whilst the mother makes her first foraging trip to sea. She will then continue to make foraging trips lasting two to eight days (McCafferty et al. 1998b), returning to feed her pup for one to two days (Boyd et al. 1994). This cycle will last until the pup is weaned in early April, approximately 120 days later. After this both females (Duck 1990; Boyd et al. 1998) and pups disperse to sea (Warren et al. in press).

### ***Population status and trends***

The fur seal population throughout the Scotia Sea region has increased rapidly since exploitation ceased in 1907 (Bonner 1968; Headland 1984). South Georgia is thought to have been a refuge for a few surviving seals, and has therefore been the major source for the rise of the current population. Between 1958 and 1970, the South Georgia population had an average annual growth rate of almost 17% (Payne 1977; Boyd et al. 1990). The colonies at Bird Island are likely to have been a source for rapid increases in seals at other locations, both on South Georgia and elsewhere in the Scotia Sea region.

The last population estimate of fur seals at South Georgia was carried out in 1990-91, it estimated a total population size of 1.5 million seals (Boyd 1993), and estimated the increase at 9.8% per year since the 1976-77 survey (Boyd et al. 1995). In 2002 the population was thought to be in excess of three million (Barlow et al. 2002). It seems likely that the population growth rate has reduced (Reid and Forcada 2005), but it would be reasonable to estimate the current population to be in excess of four million. The current population

status is the focus of a new study by the British Antarctic Survey. The population at other locations remains small, though there is some evidence of rapid population increases at Crozet Island and along the Antarctic Peninsula (Guinet et al. 1994; Whitehouse and Veit 1994; Hofmeyr et al. 1997; Bester et al. 2003).

The rate of increase at the long-term study colony at Bird Island now seems to have slowed and the population is not increasing. It seems that this and other colonies on the north-western end of the Island have now reached close to their maximum capacity (Reid and Forcada 2005).

### ***Fur seal foraging behaviour***

The distribution of Antarctic fur seals whilst at sea has been investigated using telemetry across their complete circumpolar range (for example at South Georgia: Staniland et al. 2003, Boyd et al. 2002, Boyd et al. 1998, in the Southern Atlantic: Bonadonna et al. 2001, Guinet et al. 2001 in the Indian Ocean and in the Pacific Robinson et al. (2002)). However, most studies have concentrated on lactating females and very little work has been carried out on males, non-breeding females or juveniles.

Studies on other pinniped species that have considered both genders (Kovacs et al. 1990; Hindell et al. 1991; Stewart 1997) and age (McConnell et al. 2002) classes have found marked differences in foraging behaviour. Most of this difference is likely due to differences in size either from sexual dimorphism or growth with age.

Much of our understanding of the foraging distribution of Antarctic fur seals at South Georgia comes from the satellite tracking of lactating adult

females, during the breeding season (Boyd et al. 1998; Boyd and Murray 2001; Boyd et al. 2002; Staniland and Boyd 2003; Staniland et al. 2004).

A study by Boyd et al. (2002) found that lactating fur seals from different sites at South Georgia followed a consistent pattern of travel between pupping and foraging sites, and that their choice of foraging habitat appeared to be influenced by physical oceanic gradients. It also found that lactating female fur seals foraged mainly within 100 km of the site where their offspring were located.

The distributional foraging behaviour of non-breeding or male fur seals is relatively unknown. Boyd et al. (2002a) found juvenile animals to account for over 60% of krill demand by all fur seals. Given that our knowledge to date and our extensive data sets describe the behaviour of lactating females, understanding the extent to which these data can be used to describe the distribution of the whole population is essential, and forms and the key focus of this thesis.



**Table 1.1 Antarctic fur seal fact sheet**

<b>Description</b>	<b>Details</b>
Pup at weaning, males	Mass: 17 ( $\pm$ SD 2.60) kg (Lunn et al. 1993).
Pup at weaning, females	Mass: 13.5 ( $\pm$ SD 2.05) kg (Lunn et al. 1993).
Adult males	Length: up to 200 cm, mass: 125 kg (Payne 1978).
Adult Females	Length: up to 145 cm, mass: 33.23 ( $\pm$ SD 4.97) kg (Payne 1978).
Breeding system	Polygynous (Hoffman et al. 2003)
First parturition	Three to four years (90% of females give birth at 3 or 4 years of age) (Lunn et al. 1994)
Age when males attain territorial status	Males are sexually mature at age 3 or 4 but are not recorded to hold territory until age 7 years (McCann and Doidge 1987).
Pupping/mating season	Late November to late December (median pupping date $\sim$ 4-8 Dec). Oestrus follows approximately 5-6 days after giving birth (Doidge et al. 1984). Births are highly synchronous, with 90% occurring within 21 days (Payne 1977; Duck 1990).
Gestation	Twelve months (delay of implantation of 3.5-4 0 months) (Lunn et al. 1993).
No. of offspring	One, rarely two (Lunn et al. 1993).
Weaning	April, with four months between birth and weaning (Lunn et al. 1993).
Breeding habitat	Preference for sheltered shingle beaches, but also amongst tussock grasses (McCann and Doidge 1987).
Longevity	Few reach more than 23 years, females are thought to live longer than males (McCann and Doidge 1987).
Diet	Primarily krill, but also fish (more so in males) and in lower quantities, squid, and for males, also penguins (Doidge and Croxall 1985; Reid 1995; North 1996; Reid et al. 1996; Casaux et al. 2003).
Predators	Leopard seals, though this is probably insignificant (Boveng et al. 1998).
Population size (summer at South Georgia)	Over three million (in 2002) (Barlow et al. 2002).
Population trend	Increasing (possibly stable at densest areas) (Reid and Forcada 2005).
Distribution	Breeds on the sub-Antarctic Islands, South Shetland and Orkney Islands. 96% of the population breed at South Georgia
Conservation status	Protected under the Antarctic Treaty's, Convention on the Conservation of Antarctic Seals (CCAS) (Croxall 1987).

#### ***1.2.4 Macaroni penguins***

The other main homoeothermic krill consumers at South Georgia are macaroni penguins (Barlow et al. 2002; Hewitt et al. 2004c). They are estimated to consume ~8.08 million tonnes of krill per year (Boyd 2002a). Numbers of macaroni penguins at South Georgia have been in decline for over three decades (Trathan 2004) and the population may now only be half of the five and a half million breeding pairs estimated by Croxall and Prince (1979) (Trathan et al. 1996a; Barlow et al. 2002).

During incubation foraging trips last between 10 to 26 days and both sexes travel in a northwesterly direction towards the Maurice Ewing Bank (see Figure 1.1), an area with high bathymetric variation to the northwest of South Georgia. Some individuals, particularly males, travel to the PF (Barlow and Croxall 2002b). During the chick-rearing period, the foraging behaviour of macaroni penguins is more restricted than that of Antarctic fur seals. After hatching, males brood and guard the chick, whilst females forage to bring the chick food. During this time they forage over the continental shelf (Trathan et al. in press), at an average distance of 62 km from the colony. Both males and females provide for the chick during crèche when foraging trips are more extensive.

#### **1.3 Methods to determine the distribution of animals at sea**

For important marine predators such as Antarctic fur seals and macaroni penguins, it would be useful to observe all that an animal does, all of the time, throughout its natural environment. However, this is never wholly possible, and is particularly difficult in the pelagic environment. Two

techniques are therefore regularly used to determine the distribution of predators at sea. These are:

Direct visual observation of animals at sea from a ship or aircraft (Tasker et al. 1984; Buckland et al. 1993a). This allows information to be gathered over a large area, and for all individuals present in that area. This method also permits the collection of environmental information such as the presence of other species, prey, or oceanographic variables, but has only limited potential to provide information on the status of individuals such as sex, age or reproductive status. Different behaviour may greatly alter the detectability of an animal. In one area or time, an animal may spend much of its time diving or resting, whilst in other areas and at other times they may be travelling at the surface in large groups.

The use of electronic devices allows monitoring of remote behaviour of selected demographic categories (Croxall 1995). The use of platform terminal transmitters (PTT) is common. These are satellite transmitters, attached to the animals and which can give a clear record of the animals movements at sea. These are often combined with other instrumentation, which can provide details of the local environment, such as water temperature (Boyd and Murray 2001), or further behavioural data such as recorded by time depth records (TDR) (Boyd et al. 1991), that allow a 3D picture of the animals' movements to be reconstructed (Simpkins et al. 2001). These instruments have given an insight into an individual's behaviour at sea, as well as information about its local environment (Boyd et al. 2001). This method, however, is expensive and is often restricted to a particular proportion of the population, to allow tag recovery.

Each of the above two methods have their own relative strengths and weaknesses, but an integration of approaches has potential to provide a much more powerful insight into population distribution and abundance at sea.

### ***1. Background to abundance estimation by transect survey***

In order to estimate the abundance of seals from a shipboard survey, we must:

- Representatively sample the study area.
- Accurately record the number of animals sighted.
- Estimate the proportion of animals present but not detected by the observer.

To sample the study area representatively it is essential that transects are arranged to allow for both the different habitat types and any particular gradients present (Buckland et al. 1993a). It is critical that the sample is not biased with respect to any particular biological or physical feature (Guthery 1988). Several options exist for the placement of transects. A commonly used method randomly places parallel transects (Lloyd, 1967), zigzags or a grid across the study area; however this may not be the most efficient way to reduce sampling variance and may still result in bias. A second approach is stratified random sampling (Yates 1953; Cochran 1977). This is a two-stage approach. The study area is divided into rectangles and then transects are placed randomly within the rectangles, thus ensuring a random distribution of transects but also ensuring that all differing areas of the study are represented. It is also essential that, where there is a gradient, such as bathymetry or ocean currents, transects are laid perpendicular to this (Buckland et al. 1993a).

It is sometimes assumed that the number of animals seen is a constant proportion of the population within the transect (Rosenstock et al., 2002; Thompson, 2002). Yet it is clear that detection probabilities are rarely consistent over an entire survey and may often be influenced by factors such as environmental conditions at the time of survey (e.g. sea state), or spatially and temporally specific animal behaviours. Even where only an index of abundance is required, such factors need to be considered at the level of each observation interval. In this study the decay in detection probability was considered as a result of several factors, including perpendicular distance from the transect line, the weather conditions and sea state at the time of observation and the behaviour of the target animal. Whilst these adjustments have been well documented for cetaceans, this is not the case with seals. In most open water areas, seals are patchy in their distribution, spend considerable time below the surface, and are difficult to see when they are at the surface. Consequently there are few studies where seals have been counted in open water (Buckland et al., 1993a; Hunt et al., 1992; McLaren, 1961). Of these only a few have attempted to quantify density and these have applied both line (Buckland et al., 1993a) and strip-transect (McLaren, 1961) methods.

#### **1.4 Aims and objectives**

The aim of this thesis is to quantify and describe the spatial distribution of demand for krill by Antarctic fur seals (and selected other predators) in the waters to the northwest of South Georgia. This thesis falls into three parts which characterise; (1) the number of seals, (2) the distribution of seals and (3) the demand for krill.

The specific objectives are:

- To improve methods for scaling predator count data collected from ship surveys to obtain an estimate of density, and in turn to provide a first attempt at quantifying the distribution of Antarctic fur seals from a transect survey.
- To examine some of the factors influencing the distribution of krill predators around South Georgia.
- To investigate methods for comparing distributional data generated by simultaneous direct observation at sea and by satellite telemetry of marine predators. In doing so we hope to understand if the behaviour of satellite tagged lactating Antarctic fur seals can be used as a proxy for the whole population.
- To assess the total estimated length-specific demand for krill by predators, within small-scale regions at South Georgia in relation to the available krill and in doing so provide the first spatially explicit comparison of the predator-prey balance within this key region.

### **1.5 This thesis**

Data specific to this thesis were collected at South Georgia during January and February 2002 from the research vessel RRS James Clark Ross and from the British Antarctic Survey research station at Bird Island (indicated on Figure 1.3). The field methodologies used to gather the at-sea data as well as techniques developed to scale the raw data to final density estimates, involving adjustments for distance from observer, environmental influences and dive behaviour are summarized in Chapter Two.

Chapter Three applies the methodologies developed in Chapter Two to obtain concurrent density and distribution estimates for three other krill eating species, macaroni and gentoo penguins (*Pygoscelis papua*) and Antarctic prions (*Pachyptila desolata*).

Chapter Four investigates the relationship between the distributions derived by satellite telemetry (individual approach) and by line transect (population approach), i.e. specifically, to investigate the question; can we use distributional knowledge derived from telemetry of lactating females as a proxy for the whole population? Chapter Four also develops General Additive Models to describe the distribution of seals based on the variables of bathymetric depth and slope, proximity to haul-out site and latitude and longitude. The predicted distributions from these models are then compared.

Chapter Five looks at the energetics and dietary composition of krill predators, to quantify the demand for krill within the study area, it compares these values with estimates of availability of length-specific krill, and krill growth rates. Finally, the major findings and their significance are brought together and discussed in Chapter Six.

## CHAPTER TWO

### **Use of a shipboard transect survey to determine the at-sea density of Antarctic fur seals to the northwest of South Georgia, January 2002**

#### **2.1 INTRODUCTION**

##### ***2.1.1 Abundance and distribution of marine mammals***

Understanding the spatial and quantitative relationships between predators and their prey is fundamental to understanding the operation and dynamics of any species or ecosystem. In pelagic marine systems simultaneous visual observations of predator and prey are often impossible. Generally it is only the air-breathing upper-trophic level species that are visible. Nevertheless, it has been recognised that these upper-trophic level species can play an important role as regulators of prey dynamics and indicators of change (Cairns 1987; Estes 1996; Monaghan 1996; Montevecchi and Myers 1996; Estes et al. 1998; Reid and Croxall 2001; Estes et al. 2004; Williams et al. 2004; Trathan et al. 2006).

In order to understand a species' impact on an ecosystem, information on abundance and trends in its populations is required; such information may only be available within a limited geographic area, and in the case of seals and seabirds, very often only from onshore breeding colonies. However, in order to understand the direct interactions of marine predators and their prey, we require information on the abundance of animals within a spatially restricted area, especially at spatial scales where simultaneous assessments of the



abundance of predator and prey are possible (Davoren et al. 2002; Burger et al. 2004).

One common approach to estimating the abundance and distribution of marine mammals in a given area is by visual survey conducted from an observation platform such as an aircraft or ship (Laake et al. 1997; Bibby 2000). This approach offers a relatively fast and straightforward way to provide information on the animals in a study region. This is especially so when carried out as part of a multi-disciplinary study when concurrent data describing physical and biological variables are also recorded.

The South Georgia region has a long history of scientific investigation. Since 1995 intensive multi-disciplinary cruises in the region have attempted to interpret the ecology and oceanography of the region (Atkinson et al. 2001). Previous at-sea surveys of predators in the region have been carried out but, these have only ever provided relative abundance estimates and have never attempted to calculate absolute abundance estimates (Hunt et al. 1986; Hunt et al. 1992; Trathan et al. 1998b; Reid et al. 2004). This has also limited previous estimates of krill demand in the region. Estimates of krill demand have been made (Boyd 2002a; Hewitt et al. 2004c) but they have always been based on estimates for the whole population. Future estimates of the krill supply and demand balance at South Georgia are dependent upon obtaining accurate estimates of fine-scale, area specific densities.

In 2002 the British Antarctic Survey undertook an intensive, multidisciplinary cruise in a study region to the northwest of South Georgia. The cruise attempted to quantify krill biomass, import, growth, export and

mortality through the region. As part of this, it was essential to quantify the role of krill predators, including Antarctic fur seals, in this krill-flux equation.

### ***2.1.2 This study***

There are two common methods available for at-sea surveys of marine mammals and birds, strip-transects and line-transects. The strip-transect method uses a strip of prescribed width, within which all animals are assumed to be recorded. In situations where animals are numerous and the assumptions of complete detectability across the whole strip are met, strip-transect methods offer a suitable and efficient survey technique (Burnham et al. 1985; Hone 1988; Seber 1992). Line-transect surveys are based on counts of all animals observed along a transit of a line, where the distance from the observer is used to estimate the fraction of animals in the sample area that are detected. With line-transect surveys there is an assumption that all animals on the transect line itself are observed, or that the number of animals that are undetected along the transect line can be accurately estimated.

Typically strip-transect methods have been applied to seabirds (Tasker et al. 1984; Piatt and Ford 1993; Thompson 2002) whilst line-transect methods have been applied to surveys of cetaceans (Buckland and Turnock 1992; Barlow 1995; Hammond et al. 2002; Punt et al. 1997; Carretta et al. 2001). Where sightings of animals are infrequent due to their rarity, or where the observation opportunities are dependent on the surfacing behaviour of the animal, line-transect methods may be more appropriate.

In most open water areas seals are patchy in their distribution, spend considerable time below the surface and are difficult to see when they are at the surface. In considering a survey method that is suitable for seals it is

critically important to consider the differences in at-sea behaviour of different seal species. For example it is important to consider the difference between phocid seals which spend most of their time underwater and make excursions to the surface to breath (Le Boeuf et al. 1988), and ottarid seals which typically stay at the surface and make relatively short foraging dives (Boyd and Croxall 1996a; Mattlin et al. 1998). Nevertheless, even given the relative observability of ottarid seals, there are few studies where seals have been counted in open water (McLaren 1961; Hunt et al. 1986; Hunt et al. 1992; Buckland et al. 1993c).

In the waters surrounding South Georgia, Antarctic fur seals (*Arctocephalus gazella*) are both frequent and conspicuous and previous studies have successfully surveyed their at-sea distribution around the island (Hunt et al. 1986; Hunt et al. 1992). These studies have used a strip-transect approach and have revealed information about distribution, but were not used to calculate density in the survey areas.

For many strip-transect studies the assumptions of complete detection across the strip width have not been supported. To solve this it is possible to sub-divide the strip into distance bands and to then truncate the strip to a width where the assumption is reasonable, this is however reliant on some record of the position of sighted animals within the strip.

A second and widely adopted approach is line transect sampling, in which a curve is fitted to the data describing the decay in detection probability with increasing perpendicular distance from the observer. This technique has been described in depth by Buckland et al. (1993), and is referred to as

Distance analysis. As complete detection cannot be assumed within a strip, a detection probability curve must be fitted to the perpendicular distance data.

During surveys at South Georgia, Antarctic fur seal encounter rates are high and as they are often in large groups, this makes it difficult to record the distance to individual animals or even to individual groups. Here the strip-transect approach seems more appropriate. However, the accuracy of the assumption of complete detectability across any known strip width is untested and there is potential for estimates to be less accurate than those resulting from line-transect methods. This study therefore used a hybrid strip-transect survey method that allowed both approaches to be used in analysis with subsequent comparison.

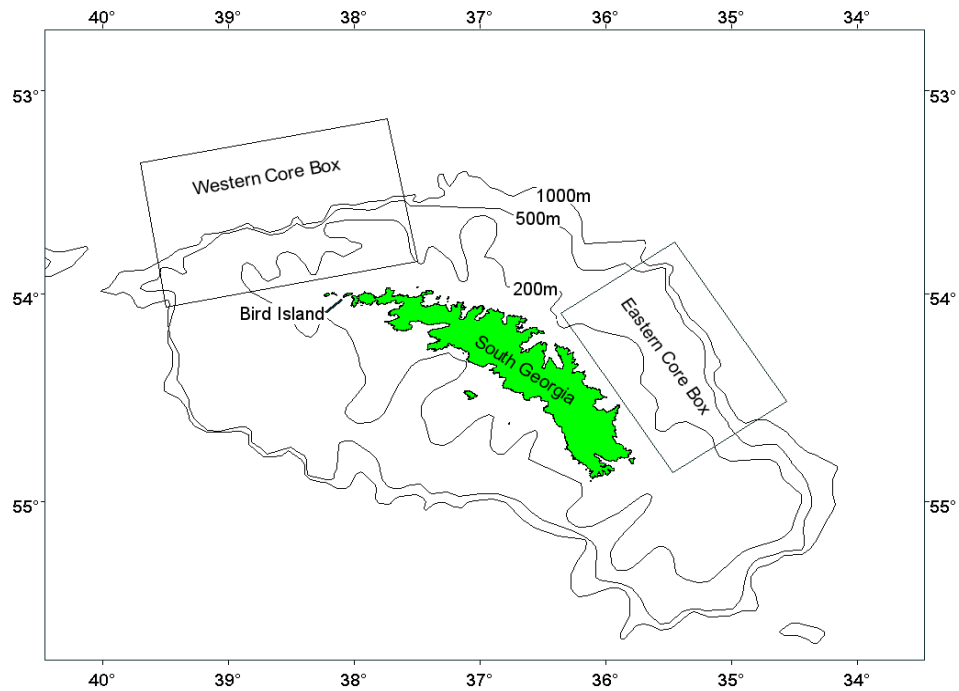
### ***2.1.3 Aims***

The aims of this study are to estimate the abundance of Antarctic fur seals in a survey area to the northwest of South Georgia. The survey was carried out in such a way as to allow comparison of and to determine the most appropriate survey methodology, balancing the relative merits of strip and line-transect methods. Behavioural data were also gathered by concurrent deployment of satellite telemetry on individuals using the study area. This allowed temporally and spatially specific, and more complex behaviour to be included in obtaining density values.

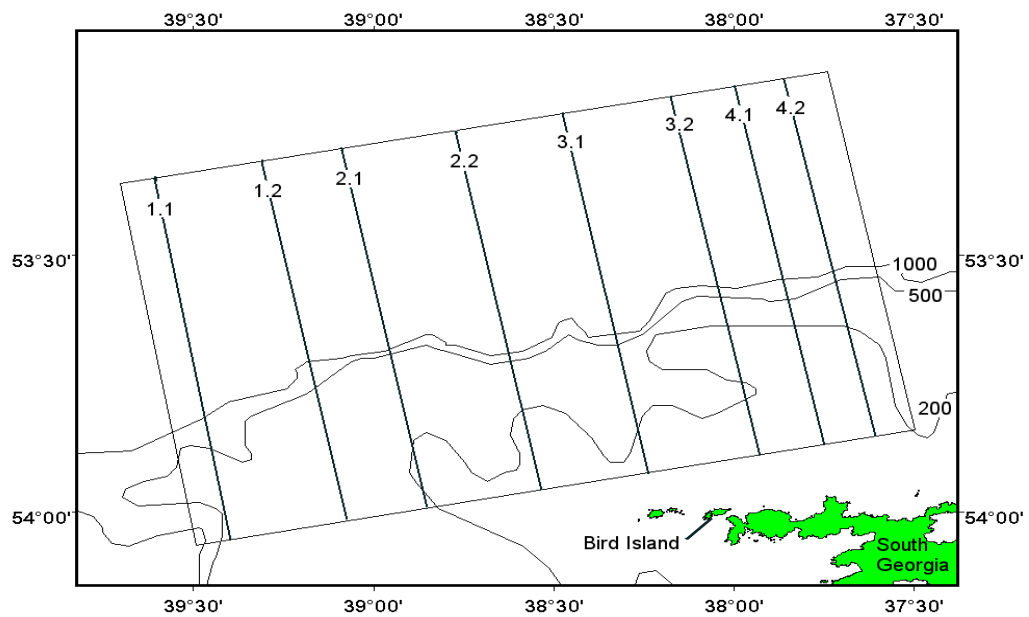
## **2.2 METHODS**

### ***2.2.1 Study area***

Since 1995 the British Antarctic Survey has carried out annual acoustic surveys to estimate krill density in two study boxes that span the continental shelf break to the northwest and northeast of South Georgia, see Figure 2.1 (Brierley et al. 1999; Trathan et al. 2003). The study described here was conducted as part of this series of multidisciplinary surveys of the Western Core Box (WCB) during January 2002. The WCB encloses a large proportion of the known foraging range of a number of krill-dependent predators, including Antarctic fur seals and macaroni penguins, breeding at the British Antarctic Survey, Bird Island study site (54° 00'S, 38° 02'W) (Barlow and Croxall 2002a; Barlow and Croxall 2002b; Staniland and Boyd 2003). The WCB measures 80 x 133 km, with an area of 10640 km<sup>2</sup>.



**Figure 2.1.** Map of South Georgia showing the western and eastern core study areas. Also shown are the 200, 500 and 1000 m depth isobaths. The WCB measures 80 x 133 km and is 10640 km<sup>2</sup> in area.



**Figure 2.2.** Map showing the layout of transects within the Western Core Box. Also shown are the 200, 500 and 1000 m depth isobaths.

The position of the survey transects (Figure 2.2) was based on the assumption that in order to adequately survey the krill population, the location of each transect should include the full range of habitat types, from on-shelf to oceanic water.

To satisfy the requirement for random selection of transects within the study area whilst avoiding the possibility of a very uneven distribution of sampling effort, a two-stage procedure was used (Yates 1953; Cochran 1977). The study area was divided into eight parallel strips of equal width and a transect was placed randomly within each strip. This procedure achieved an ecologically appropriate distribution of survey effort whilst ensuring that each potential transect location had an equal probability of being surveyed. This sampling design was established to gain robust estimates of krill density (Brierley et al. 1999).

For acoustic surveys of krill the transect is used as the sampling unit and makes no assumptions about the distribution of observations within individual transects (Jolly and Hampton 1990b). Since the survey was designed to produce a statistically robust estimate of krill density it was considered to be an equally appropriate design to produce an estimate of fur seal density.

### **2.2.2 Survey methods**

Predator observations were made from a sheltered, outside position on the top deck of the *RRS James Clarke Ross* with an observer eye level at 18.5 m above sea level. Three observers were normally present, with one highly experienced primary observer (CJ Camphusen). The roles of secondary observer and recorder were rotated regularly. All observations were recorded

onto pre-printed sheets and were entered into a computerised database at the end of each survey day. The whole survey was repeated twice, with a five-day gap between the two surveys; these are referred to as the first and second surveys.

Observations were made over a notional area, 300 m forward and to one side of the ship, which maintained a nominal speed of 10 kts. Sightings were recorded in one of four distance bands parallel to the ship track (0-50 m, 51-100 m, 101-200 m and 201-300 m) (see Figure 2.10). Distance from the vessel was determined using observer eye height above sea level and distance to the horizon. This was marked out on a measuring gauge a fixed distance from the observer. Observations were made continuously and were summed into five-minute periods, following the methodology of Tasker et al, (1984) as adapted by Van Franeker (1994) and were analogous to those used in previous studies of the at-sea distribution of marine predators in this region (Hunt et al. 1986; Hunt et al. 1992; Van Franeker 1994; Whitehouse and Veit 1994; Trathan et al. 1998b; Mehlum 1999).

Sea state was recorded at 30-minute intervals, or where a noticeable change took place, using the Beaufort wind speed and sea state scale (



Table 2.1). In sea states greater than six, or in severe glare (i.e. when the ship was heading towards the sun), observations were discontinued. Where fog reduced visibility to between 200 and 300 m, the transect width was reduced to 200 m. Observations were discontinued if visibility was reduced below 200 m.

**Table 2.1. Beaufort winds speed and sea state scale (Beaufort 1832; Watts 2004).**

Sea State	Wind speed (Kn)	Description
0	<1	Like a mirror
1	1-3	Ripples, but none form crests
2	4-6	Small wavelets, crests do not break
3	7-10	Large wavelets, odd scattered white caps
4	11-16	Small waves, fairly frequent white caps
5	17-21	Moderate waves, many white caps
6	22-27	Large waves beginning to form, probably spray

### ***2.2.3 Accounting for seals that are not detected***

The number of animals actually observed as a proportion of those present might be influenced by six primary factors: observer fatigue, distance from the transect line, seastate, animals diving and hence not being visible to the observer, visibility and group size. The way these factors were included in the analysis are discussed below. In this section of the methods, some results have being included where they pertain to the calculation of adjustment factors that were used to produce the estimates of density. The results of these correction factors in the estimation of density are dealt with solely in the results.

#### ***1. Observer fatigue***

Observer experience and ability can have significant influence on the numbers of animals sighted (VanderMeer and Camphuysen 1996). As this was a single platform survey, with a single group of observers, no estimate of observer error was possible. Observer fatigue may be reflected in altered detection rates or reduced count accuracy. Therefore, any significant change in predator abundance or distribution over each four-hour observation period could be evidence of observer fatigue; comparing the density and variance

values between the first and second half of each four-hour observation period allowed this to be checked for.

## ***2. Distance from the observer***

The probability of detecting an animal will decrease as a function of distance from the observer. The two methods of dealing with this are either to estimate a function that describes the decay of observation probability with distance from the transect line; or to truncate the transect width to a distance where the assumption of complete detection is realistic.

### ***2a Estimating the detection function***

The DISTANCE software (RUWPA, Buckland et al., 1993), was used to estimate the detection probability function. The probability of detecting an object given its perpendicular distance ( $y$ ) from the transect line, is termed  $g(y)$ , calculated from the probability density function,  $f(y)$ , rescaled so that its maximum value (at zero distance) is equal to one (Buckland et al., 1993). The detection function  $f(y)$  was based on a model that fits the decay in detection probability as a function of perpendicular distance from the transect line.

Buckland et al. (1993) proposed a number of models that are combinations of key functions, see Figure 2.3, and series expansions. These models have specific properties, making them suitable for certain types of decay function. Series expansions are used to adjust the key function, such that adjusting one or two parameters improves the fit of the model.

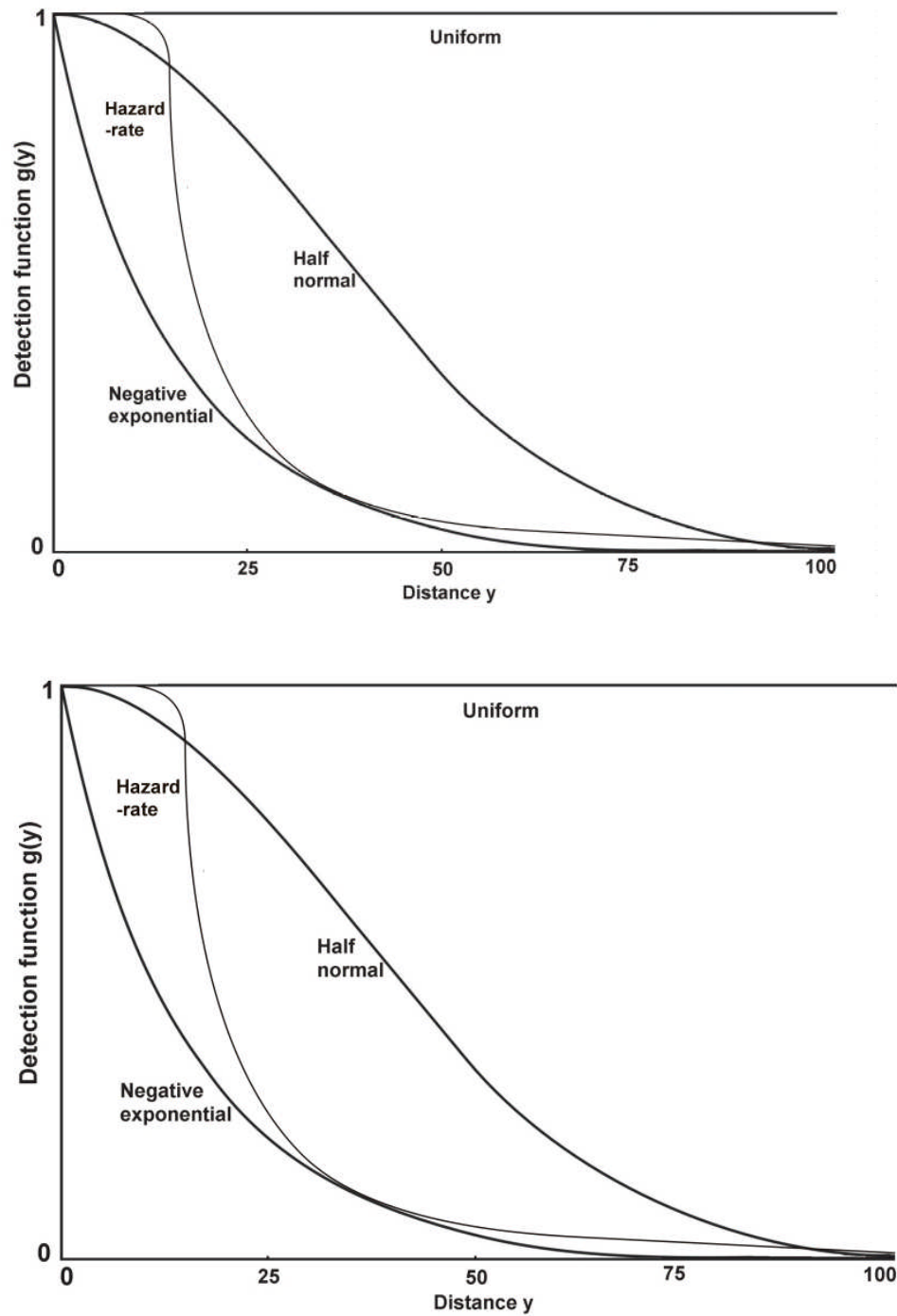
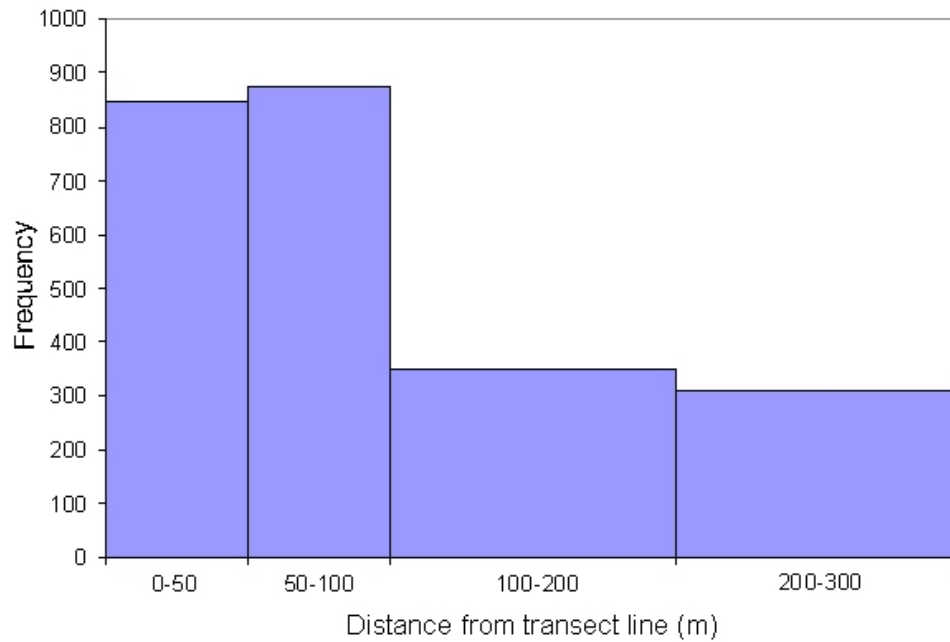


Figure 2.3. Key functions useful in modelling distance data. After Buckland et al. (1993a).



**Figure 2.4. Frequency histogram of Antarctic fur seal sightings in perpendicular distance bands; data are pooled for both surveys. South Georgia, January 2002.**

As can be seen in Figure 2.4, the survey data have a large shoulder, with detectability greatly reduced beyond the 100 m distance band. This shoulder is common to many ship surveys.

One function often suited to this distribution of data, is the hazard-rate function in which, by adjusting parameter  $b$ , the shoulder of the curve can be extended outwards along the  $x$ -axis,  $\sigma$  represents the scale model of the hazard rate model.

$$\text{Hazard rate model} = 1 - \exp(-(y/\sigma)^{-b}) \quad \text{Equation 2.1}$$

In this case however, due to the low number of available fitting parameters, i.e. only four distance bands, it proved difficult to fit this curve, and an abnormally high variance estimate resulted, see Table 2.2. A second

model offering a good fit to the data was the half normal model. This, combined with a cosine series expansion provided a good fit to the data.

$$\text{Half-normal model} = \exp(-y^2 / 2\sigma^2) \quad \text{Equation 2.2}$$

$$\text{Cosine series expansion} = \sum_{j=2}^m a_j \cos\left(\frac{j\pi y}{w}\right) \quad \text{Equation 2.3}$$

Where  $w$  = distance from the transect line and  $a_j$  = the surveyed area of the  $j^{\text{th}}$  transect.

Both models were explored for their fit to the data collected. Choice of model was first done by visual inspection of the fit of the function to the data and how these fits could be improved by the adjustment parameters. Akaike's Information Criterion (AIC), was then used as a further selection criterion (Buckland et al. 1993a). The aim of the AIC is to find the function with the best fit without having an excessive numbers of parameters i.e. the most parsimonious model. The best model will have the lowest AIC value.

The AIC function is defined as:

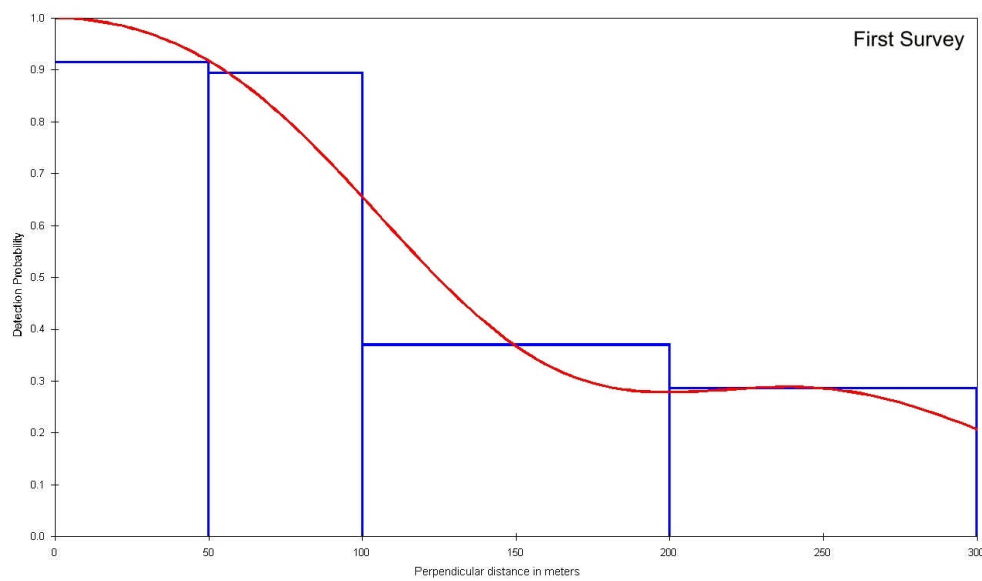
$$AIC = -2.\log_e(L) + 2q \quad \text{Equation 2.4}$$

Where  $\log_e(L)$  is the log-likelihood function evaluated at the maximum likelihood estimates of the model parameters; and  $q$  is the number of parameters in the model.

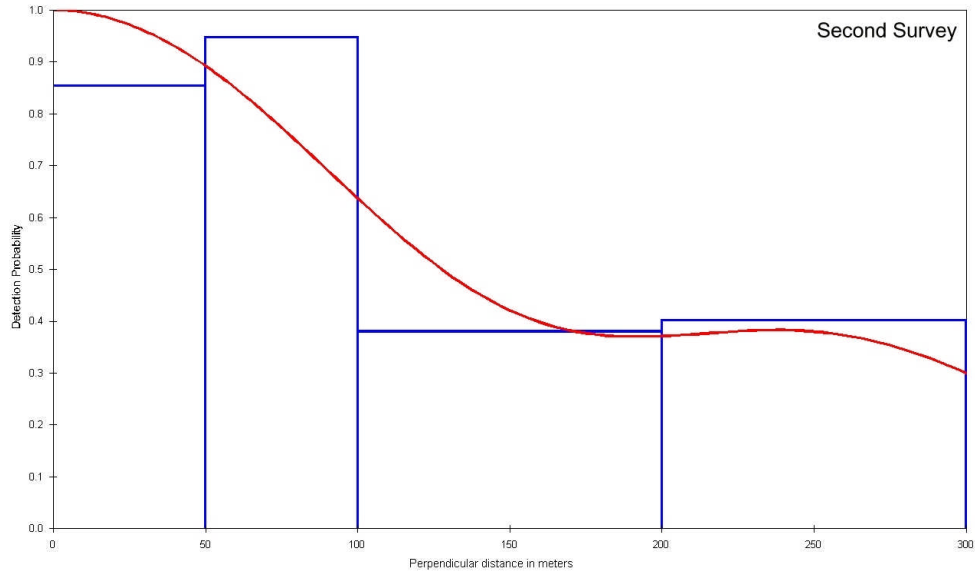
**Table 2.2. Properties of the different probability detection functions, fitted for both surveys combined.  $n=1539$  CV is for the detection probability ( $P$ ).**

Key Function	Adjustment	AIC	$P$ ( $\pm$ 95% CI)	Total parameters	CV (%)
Half-normal	Cosine	3881	0.54 (0.48, 0.60)	3	5.61
Hazard rate	Polynomial	3900	0.56 (0.50, 0.62)	2	5.44
Hazard rate	Cosine	3880	0.52 (0.02, 1.00)	1	370.00

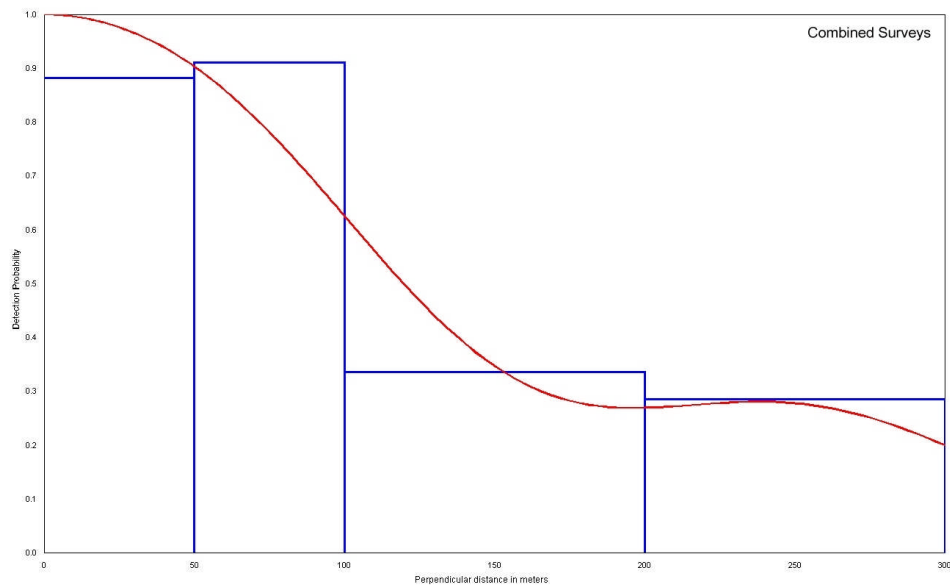
Table 2.2 shows the AIC and detection probability for the best fitting models. Due to the low number of possible parameters and the constraints placed on the hazard-rate model, particularly with cosine adjustments, this model resulted in unrealistic variance estimation. The half-normal model, with cosine expansion was finally selected; the fit of this can be seen in Figures 2.5, 2.6 and 2.7. for the first second and both surveys combined.



**Figure 2.5. Sightings distribution of Antarctic fur seals against perpendicular distance bands for the first survey. The data were fitted with a half-normal function; with cosine adjustment parameters. The curve fitted indicates the estimated detection probability.  $n = 747$ ,  $p = 0.52$ ,  $\pm 95$  CI 0.45, 0.60;  $f(0) = 0.0064 \pm 95\%$  CI 0.0055, 0.0074.**



**Figure 2.6.** Sightings distribution of Antarctic fur seals against perpendicular distance bands for the second survey. The data were fitted with a half-normal function; with cosine adjustment parameters. The curve fitted indicates the estimated detection probability.  $n = 792$ ,  $p = 0.56$ ,  $\pm 95$  CI 0.48, 0.65;  $f(0) = 0.0059 \pm 95\%$  CI 0.0051, 0.0069.



**Figure 2.7.** Sightings distribution of Antarctic fur seals against perpendicular distance for both surveys combined. The data were fitted with a half-normal function; with cosine adjustment parameters. The curve fitted indicates the estimated detection probability.  $n = 1539$ ,  $p = 0.54$ ,  $\pm 95$  CI 0.48, 0.60;  $f(0) = 0.0063 \pm 95\%$  CI 0.0046, 0.0085.

Figure 2.6 shows a slightly lower detection probability in the distance band nearest to the observer during the second survey. This is often



suggestive of ship avoidance. This was not accounted for in subsequent analysis, though it is discussed later.

DISTANCE was applied to data where observations were not recorded as distinct groups or as individuals but were grouped over five minute periods for each distance band. Although this limited the full application of the DISTANCE package, it was not a problem in terms of final density or variance estimation. Specifically, because:

Sightings were grouped into four distance bands rather than a measured distance to each animal, the number of parameters usable in the distance model was therefore reduced. Thus, models had to be constrained to maintain monotonicity; this in itself was not a problem, but it did mean that sea state could not be incorporated as a covariate in the model because it is not possible to constrain for monotonicity (i.e. restricting the model that the probability curve ( $y$ ) can not increase with increasing distance from the observer ( $x$ )) in the multi-covariate model. For this reason observations were adjusted for sea state prior to curve fitting. This allowed the variance resulting from adjustments for sea states to be incorporated into the final DISTANCE model.

Observations were not recorded as distinct groups or as individuals, which meant that no interpretation could be made of how detectability was affected by group size. The expectation was that the detectability of larger groups would be less affected by distance from the transect line.

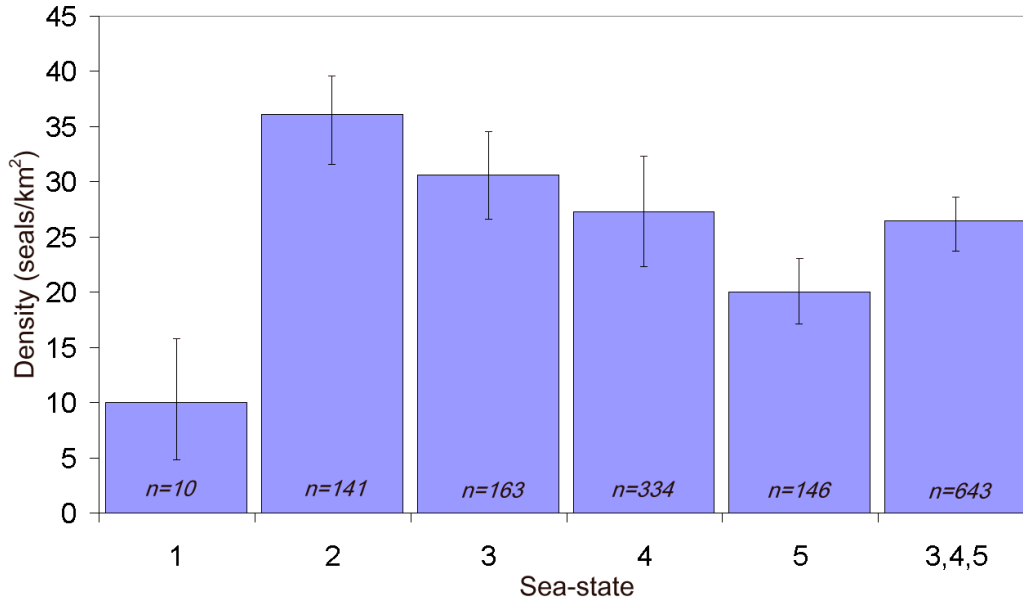
### ***2.b. Truncating the data***

Strip-transect methods make the assumption that all animals are detected, or at least that the detection probability is equal over the entire

transect width. Where data suggest this is not the case the strip can be truncated to a width at which there is no appreciable decay in detection probability; this truncation will inevitably reduce the total sample area and sample size.

### ***3. Accounting for the effects of sea state***

One common method of dealing with the effect of sea state is to survey only when conditions are such that the influence of sea state is minimised i.e. limit surveys to periods of calm weather (Buckland et al. 1992; Macleod et al. 2003). However, only where survey time is inexpensive, flexible or such conditions are common is it realistic to limit survey effort to such times. At South Georgia, periods with calm seas and clear visibility are infrequent and ephemeral. In addition, being part of a multi-disciplinary survey means that flexibility over survey time was highly restricted. Therefore in this study, surveys were conducted in a range of sea states and it was necessary to quantify the influence of this on detection rates.



**Figure 2.8** The mean density of seals in each observation period for each Beaufort sea state, and the mean of sea states 3, 4 and 5 combined. Error bars indicate 95% confidence intervals.

The detectability of animals decreased significantly between observations made in sea state two and those made in conditions greater than two (Mann-Whitney U test,  $p = <0.001$ ,  $n = 643$ ,  $W = 66742$ ) (Figure 2.6).

Sea state zero was not experienced during the survey and only a very small number of observations were made during periods of sea state one, and these were in an area of low density and hence had a low observed densities. Since the Beaufort sea state scale is categorical it is not appropriate to extrapolate through to a nominal sea state zero. A scaling factor to adjust the observation data to a notional sea state two was generated where:

$$p = \frac{N_{B_3} + N_{B_4} + N_{B_5}}{N_{B_2}} \quad \text{Equation 2.5}$$

Where  $N$  = the density of seals observed at  $B_i$ , the Beaufort sea state.

The Scaling factor was applied as:

$$D_a = \frac{D_u}{p} \quad \text{Equation 2.6}$$

Where  $D_a$  = the adjusted density,  $D_u$  = the unadjusted density and  $p$  = the probability of detection.

Implicit in the use of this scaling is the assumption that sea state did not influence the actual number of animals in the study area i.e. there were as many animals available to be seen in higher sea states as there were in lower sea states.

**Table 2.3. Densities of animals sighted under different Beaufort sea state conditions and scaling multiplier used to adjust sightings of sea states >2 to notional Beaufort sea state 2. Un-truncated applies to sighting data from the full 300 m strip width, whilst truncated applies to sightings data only within the nearest 0-100 m distance band.  $n$  is the number of observation periods and mean is the arithmetic mean seal density (seals km<sup>-2</sup>) See text for methods.**

Data set	Sea state	$N$	mean	Lower 95% CI	Upper 95% CI	Scaling probability
Truncated	Sea state 2	141	36.09	28.88	43.31	0.733
	Sea state 3 – 5	643	26.46	21.43	31.49	
Un-truncated	Sea state 2	141	23.52	19.40	27.64	0.710
	Sea state 3 – 5	643	16.70	14.09	19.44	

#### **4. Accounting for diving animals**

Some seals may be below the water surface at the time that observations are made and hence would be unobservable (Barlow, 1987; Barlow, 1995; McLaren, 1961). This problem has been addressed for cetaceans, using corrections derived from simulation models based on expected dive behaviour and observer search behaviour (see Barlow, 1993). Antarctic fur seal dive duration is shorter than that for cetaceans and the observer search area is, in comparison to the line transect approach applied to cetaceans, restricted.

For the purposes of correcting for diving, a seal within the visual range of the observer which does not dive had a detection probability equal to one (this may not be the case, but this assumption is dealt with by other correction factors), and, a seal that is below the surface had a probability of zero. However, where seals dive during the observation period then the probability of being seen is a function of the average dive duration,  $u$ , and the period of time during which an area of the water surface is within the visual range of the observer,  $t$ , see Equation 2.8.

The influence of dive behaviour on the detectability of seals was based on a model with two main components (1) the relative proportion of time an animal spends continuously at the surface or in a diving bout and (2) the probability of detecting a animal involved in either of these behaviours. Thus, overall the probability of sighting an animal,  $P$ , is:

$$P = (T_s p_s) + (T_d p_d) \quad \text{Equation 2.7}$$

Where  $T_{s, d}$  = the proportion of time spent at the surface or within a diving bout respectively, and  $p_{s, d}$  is the probability of detecting an animal that is either at the surface or within a diving bout respectively.

$p_s = 1$  and  $p_d$  is calculated as:

$$p_d = \frac{t}{u} \quad \text{Equation 2.8}$$

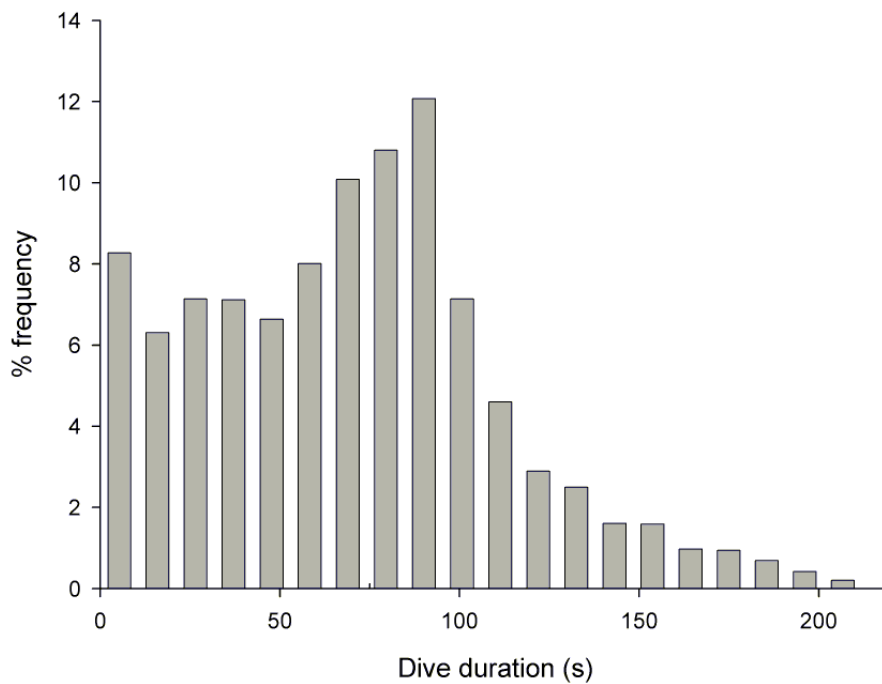
Observed duration,  $t$ , and the dive duration,  $u$ , were both non-normally distributed and hence could not be described by their means. Variables in this model also carry some degree of uncertainty. For these reasons parameter values and their variance were incorporated using Monte Carlo simulation. This method incorporates uncertainty for each variable into the final estimate.

In each run of the model, parameter values were randomly selected from empirically derived data. Thus, multiple runs of the model produced a distribution of sighting probabilities.

### ***Describing dive behaviour***

Dive behaviour of males and juvenile Antarctic fur seals has not been described. However, behaviour of lactating female Antarctic fur seals foraging from Bird Island has been described extensively (Boyd & Croxall, 1992; Boyd et al., 1991; Boyd et al., 2002; Boyd et al., 1994; Boyd et al., 1998; Croxall et al., 1985; McCafferty et al., 1998a; Staniland & Boyd, 2003; Staniland et al., 2004). Overall mean dive duration ( $u$ ) has often been found to be less than one minute, although dive behaviour has been shown to differ in relation to the foraging area and time of day (Staniland & Boyd, 2003; Staniland et al., 2004). The longest dives occur inshore during the day time, the same time as this survey was carried out.

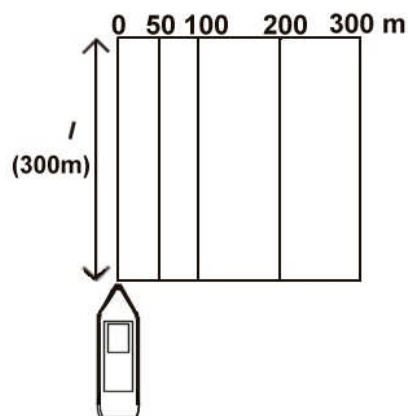
In order to produce an appropriate correction for dive behaviour, data from 28 time-depth recorders (TDRs) (dimensions 9.5 x 2.5 x 2.5, 50 g, Mk VII, Wildlife Computers) deployed on lactating female Antarctic fur seals from Bird Island were used to produce a frequency distribution of dives (Figure 2.9). TDRs were programmed to sample dive depth ( $\pm 1$  m) at two-second intervals. Dives shallower than two meters were not included in the analysis. Only dives that occurred during the times when observations were conducted (during daylight hours) were included in the analysis of dive durations (see Figure 2.9).



**Figure 2.9.** Frequency distribution of daytime dive durations (s) for lactating female Antarctic fur seals foraging from Bird Island, January 2002.

### *Describing observation time*

The period of time that a section of the waters surface is under observation ( $t$ ) is the time taken to travel the length of the area of observation,  $l$ , as indicated in Figure 2.10. (in this case  $l = 300$  m).



**Figure 2.10.** Diagram showing observation area and perpendicular distance bands, in relation to the survey vessel.

It can be seen from Figure 2.10 that where  $l$  is the extent of the survey area ahead of the vessel and  $v$  is the speed of the ship, then the length of time,  $t$ , that a point can be kept under surveillance is:

$$t = \frac{l}{v} \quad \text{Equation 2.9}$$

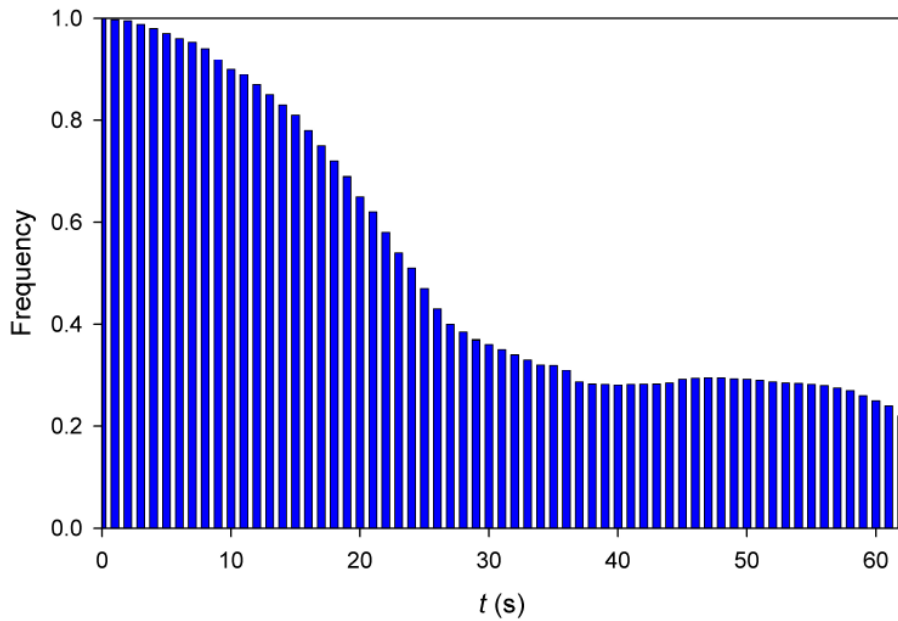
Here  $v = 4.9 \text{ m s}^{-1}$  and  $l = 300 \text{ m}$ , therefore for this study,  $t = 61.22 \text{ s}$ .

We know from investigating the decay in detection probability with increasing perpendicular distance from the observer that the probability of detection decreases with increasing distance from the observer. Sideways detectability was measured, but the same decay is likely to be present forward from the observer as it is to the side (Figure 2.7). This means that we can not assume complete detectability over distance  $l$ .

The intercept of the decay curve (Figure 2.7) between the  $y$  and  $x$  axis ( $y$  = probability of detection,  $x$  = distance from the observer) can be interpreted such that  $y$  = the proportion of observations at that distance that are detected and  $x = t$ .

By dividing the area under the curve into one-second time bins (where distance in meters was converted to represent time in seconds (Equation 2.9)). The proportionate frequency of the results values gave the proportions each bin value should make of the overall source population of  $t$  values for the model, see Figure 2.11.

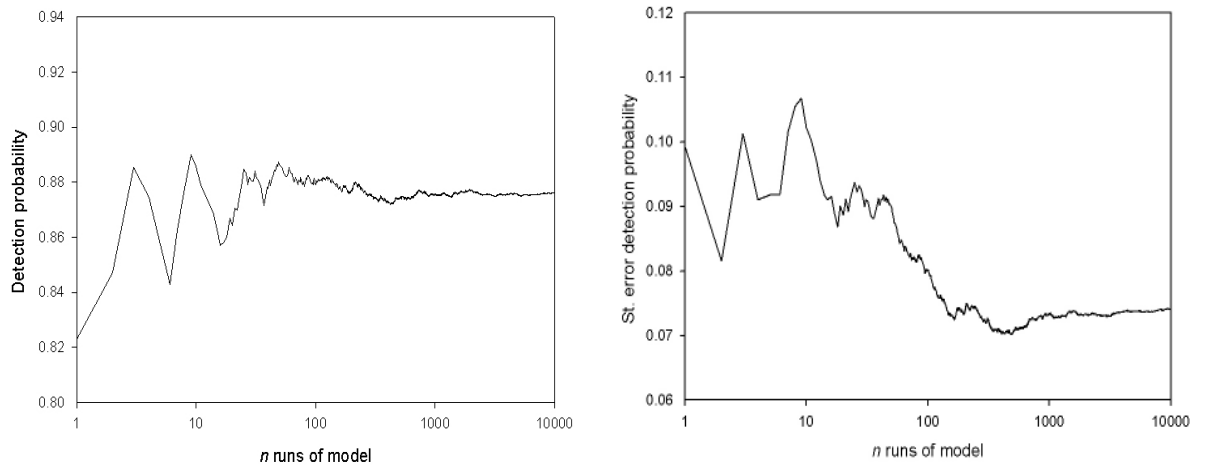




**Figure 2.11.** Frequency distribution (proportion) of observation periods ( $t$ ) with complete forward detection probability. The shape of the distribution is based upon the DISTANCE decay curve estimated for sideways detection probability.

### *Incorporating variability*

The variables incorporated stochastically into the Monte Carlo dive model were the proportion of time spent diving ( $T_d$ ) and at the surface ( $T_s$ ) where  $T_d = 0.21$  with a uniform error distribution ( $\pm 0.10$ ) and  $T_s = 1 - T_d$ . Dive duration ( $u_i$ ) was drawn randomly with replacement from a population of 10000 values representing the real population of dive durations (of which the arithmetic mean was  $76 \pm 17.6$  SD). Observation duration ( $t$ ) was drawn randomly from a population of 10000 values representing the area underneath the DISTANCE generated curve.



**Figure 2.12. Results of dive model showing the influence of diving on detection probability and its associated standard error over 10000 runs of the model.**

The model result and its associated standard deviation stabilised at near to 1000 runs of the model (Figure 2.12). When run over 10000 iterations, the model found detection probability as a result of dive behaviour to be 0.876 ( $SD \pm 0.074$ ) this probability was therefore applied to the complete data set in the same way described for the sea state adjustment factor.

### ***Sensitivity analysis***

Sensitivity analysis of the model was carried out by systematically incorporating uncertainty deriving from each variable ( $T_d$ ,  $t$ , and  $u$ ), whilst holding the others constant at their deterministic values, and assessing the proportion of the variance coming from the variable in question. Also investigated was the effect of independently varying the input variables on the final output value. The average value of the input variable was increased or decreased by 10% whilst maintaining other components constant at their deterministic values.

**Table 2.4. Variation in detection probability of Antarctic fur seals associated with each variable, when present in the dive model as the only variable with uncertainty, expressed as a proportion of the total variance in detection probability. Also shown is the sensitivity of detection probability to a 10% change in the average value of the input variables. A negative value indicates when the change in probability was opposite to the direction of change in the value of the variable.  $n$  iterations of model = 1000. See text for methods.**

<b>Variable in which uncertainty was incorporated</b>	<b>%CV of variable</b>	<b>Proportion of total variance explained</b>	<b>Sensitivity (<math>\Delta\%</math>)</b>
Proportion of time spent diving ( $T_d$ )	15.08	0.16	-1.76
Observation duration ( $t$ )	56.18	0.37	0.82
Dive duration ( $u$ )	61.51	0.48	-0.74

Though accounting for only 16% of the overall variance (Table 2.4), sensitivity analysis revealed the model to be most sensitive to the total proportion of time spent diving. A 10% change in  $T_d$  resulted in a  $-1.76\%$  change in the final values. This value is the most influential on the final model results. Observation duration and dive duration both had higher influence on total variance (0.37 and 0.48 respectively), but a 10% change in their value had a lower influence on the resulting probability, (0.82,  $-0.74\%$  respectively). Overall it should be considered from these results that the model was quite insensitive.

#### ***Other factors influencing detection probability***

Movement of animals in response to the vessel is a problem for many transect surveys, with animals attracted to or repelled by the vessel, potentially causing large bias (Barlow, 1995; Palka & Hammond, 2001; Turnock & Quinn, 1991). Here this is considered qualitatively by looking for unexpected shapes in the distance from observer/detectability curves (Buckland et al., 1993b) and by recording animal behaviour and swim

direction at first sighting, as well as noting any obvious change in behaviour in response to the vessel.

#### 2.2.4 Describing the mean and variance

The arithmetic mean and variance were calculated as recommended by Jolly and Hampton (1990), using a ratio estimate similar to that described by Cochran (1977). The mean density of  $d_i$ , of seals within the  $i$ th transect was estimated using

$$d_i = \frac{c_i}{A_i} \quad \text{Equation 2.10}$$

Where  $c_i$  is the observed count of seals, and  $A_i$  was the survey effort ( $\text{km}^{-2}$ ) in the  $i$ th transect.

This is different to that used for estimates of krill abundance where each transect is weighted simply by its length (assuming constant survey effort). Here transects are weighted by total area sampled and hence also incorporate periods where transect effort was reduced from 300 m to 200 m strip width.

The density of each transect was then weighted by a ratio estimate, i.e. adjusted for the survey effort in that transect in relation to the mean effort per transect to produce a weighted transect mean,  $D_i$ , as:

$$D_i = \left( \frac{A_i}{\bar{A}} \right) d_i \quad \text{Equation 2.11}$$

The mean density,  $D$ , for the study area was then estimated from the ratio adjusted densities per transect (Cochran, 1977);

$$D = \overline{D_i} \quad \text{Equation 2.12}$$

Variance was calculated as:

$$V(D) = \frac{\sqrt{\sum (d_i - D_i)^2 \frac{A_i^2}{A}}}{n_i(n_i - 1)} 100 \quad \text{Equation 2.13}$$

Variance was described as the coefficient of variation for the weighted transect means,  $D_i$ :

$$CV(D) = \frac{\sqrt{V}}{D_i} 100 \quad \text{Equation 2.14}$$

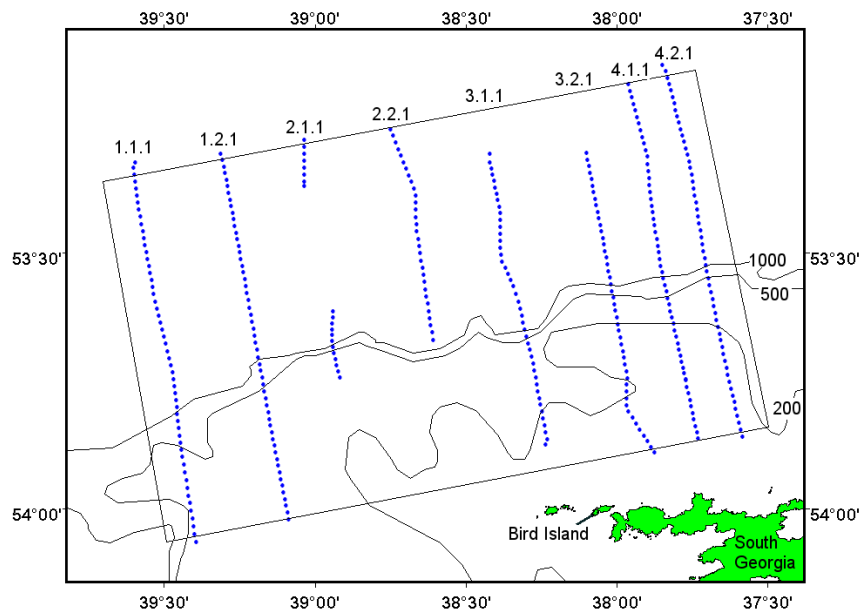
Variance was also estimated with a non-parametric bootstrap (Efron, 1979) using the transect density ( $D$ ) as the resampling unit. A function was written in MATLAB (The Mathworks Inc., 2003) to sample transect effort ( $A$ ) and un-weighted density values ( $d_i$ ) were selected randomly and with replacement to generate weighted transect density ( $D_i$ ). This was run 1000 times to produce estimates of CV for the estimates of  $D_i$ , such that:

$$\text{Bootstrapped CV } (D) = \frac{\sqrt{V}}{\bar{D}_{i(1-1000)}} 100 \quad \text{Equation 2.15}$$

## 2.3 RESULTS

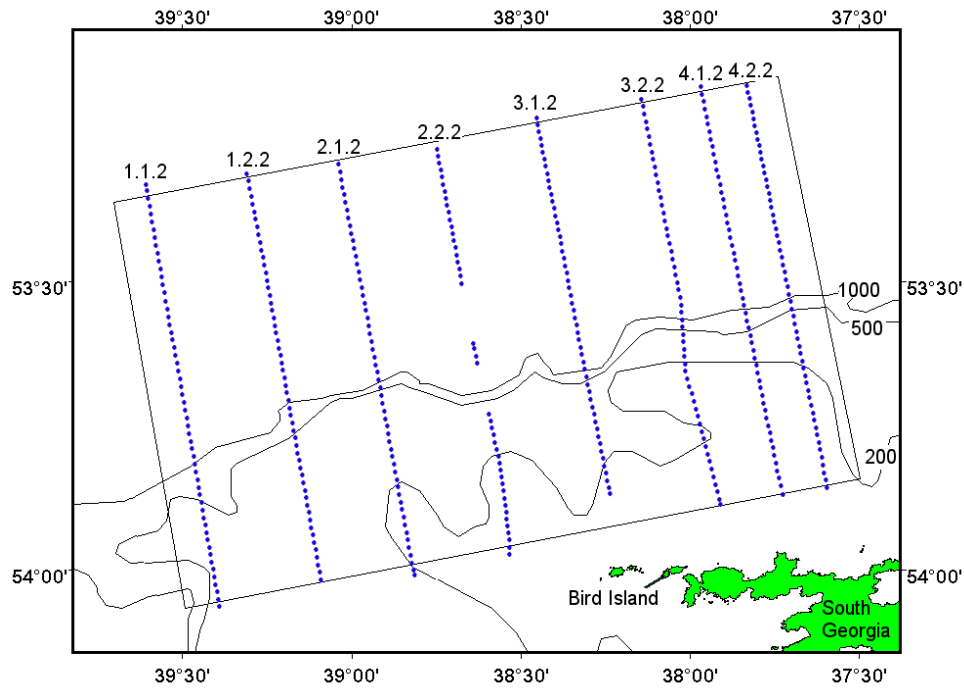
### 2.3.1 Survey coverage

Overall 87% of the planned transect length was successfully surveyed and, with the exception of a small section of transect 2.2, all transects were surveyed at least once. The final distribution of survey effort is shown in Figure 2.13 and Figure 2.14, and survey effort in Table 2.5. Due to bad weather, surveying of transects 4.1 and 4.2 on the first WCB survey was delayed; and these transects were not surveyed until the day before the second survey. This left only five days between surveys of these transects. Total survey effort was 349 km<sup>2</sup> within the WCB, 3.28% of the 10640 km<sup>2</sup> study area. Ship speed was lowered along some transects as a result of fog or ice, this is reflected in the ratios of transect length to number of five-minute observation periods.



**Figure 2.13.** Map showing survey effort during the first survey of the WCB, January 13, 14, 15 and 23<sup>rd</sup>. Also shown are the 200, 500 and 1000 m depth isobaths.

During the first survey 79% of the available transect length was surveyed. Transects 2.1 and 2.2 were particularly disrupted, as well as the northern end of transects 3.1 and 3.2, see Figure 2.13. Overall survey effort is summarised in Table 2.5.



**Figure 2.14.** Map showing survey effort during the second survey of the WCB, January 24<sup>th</sup> to 28<sup>th</sup>. Also shown are the 200, 500 and 1000 m depth isobaths.

During the second survey 95% of the available transect length was surveyed, with the only gaps in survey effort being around the shelf break, and just to the north, along transect 2.2, see Figure 2.14. Overall survey effort is summarised in Table 2.5.

**Table 2.5. Summary of survey effort and transects.**

<b>Transect</b>	<b>Date</b>	<b>Effort (km<sup>2</sup>)</b>	<b>N 5 min. periods</b>
<b>First survey</b>			
1.1.1	13/01/02	25	54
1.2.1	13/01/02	23	55
2.1.1	14/01/02	6	20
2.2.1	14/01/02	13	31
3.1.1	15/01/02	20	44
3.2.1	15/01/02	21	47
4.1.1	23/01/02	25	56
4.2.1	23/01/02	25	56
Mean		19.75	45.38
Total		158	363
<b>Second survey</b>			
1.1.2	24/01/02	25	56
1.2.2	24/01/02	24	55
2.1.2	25/01/02	25	55
2.2.2	25/01/02	19	45
3.1.2	26/01/02	23	53
3.2.2	26/01/02	25	55
4.1.2	27/01/02	25	55
4.2.2	27/01/02	24	57
Mean		23.75	53.88
Total		190	431

### 2.3.2 Observer fatigue

There was no evidence of altered density or variance values between the first and second half of each transect, (density: ANOVA  $f_{(1,30)} = 0.05$ ,  $p = 0.82$ . variance: ANOVA  $f_{(1,30)} = 0.19$ ,  $p = 0.78$ ).

### 2.3.3 Density estimates

#### *Correcting density estimates*

The uncorrected mean density of seals was 19 seals km<sup>-2</sup> and 16.48 seals km<sup>-2</sup> for the first and second surveys respectively. Correction for distance from observer by strip width truncation produced estimates of 32 seals km<sup>-2</sup> (an increase of 67%) for the first survey and 24 seals km<sup>-2</sup> (an increase of 47%) for the second survey. Correction using the decay-curve



method produced density estimates of 33 seals km<sup>-2</sup>, (an increase of 73%) for the first survey and 26 seals km<sup>-2</sup>, (an increase of 59%) for the second. There was no significant difference between the density values derived using the truncation and decay function methods within the first survey (Mann-Whitney *U*-test,  $W= 67.0$ ,  $P= > 0.05$ ) or the second survey (Mann-Whitney *U*-test,  $W= 69.0$ ,  $P= > 0.05$ ).

There was a difference in the proportionate increase in seal density between the first and second survey. This was due to a difference in the relative frequency of animals in the outer distance bands, i.e. whilst 56% of all observed animals were nearer than 100 m from the observer for the first survey, only 46% were nearer during the second, this is shown in Figures 2.6 and 2.7. As a result, the proportionate increase, when adjusted for distance from observer, is lower during the second survey. Here the decay function and truncation methods responded slightly differently, with a 47% increase using the truncation method and a 59% increase using the decay function. The difference in density when using the truncation is a response to the proportion of the total number of seals observed within and outside of the truncation distance i.e. where 100% of all observations were inside the truncation distance no increase would be expected upon truncation, where 50% are inside, an increase of 50% would be expected. The decay-function however is more sensitive and is fitted to the distribution of observations into all the distance bins recorded.

#### ***Correction for sea state***

Adjustment for sea state had a similar effect where applied with the truncation method, increasing density to 36 seals km<sup>-2</sup> (12.5% increase) for

the first survey and 28 seals  $\text{km}^{-2}$  (16% increase) for the second; or with the decay-function method, increasing density to 35 seals  $\text{km}^{-2}$  (6% increase) for the first survey and 28 seals  $\text{km}^{-2}$  (8% increase) for the second.

Following adjustments for sea state there was no significant difference between the truncated and decay curve data for the first survey (Mann-Whitney  $U$ -test,  $W= 53.0$ ,  $P= > 0.05$ ) or the second survey (Mann-Whitney  $U$ -test,  $W= 57.0$ ,  $P= > 0.05$ ).

### ***Overall density estimate***

Following adjustments for distance from the observer, sea state and dive behaviour (a uniform increase of 14%), final density values were 43 seals  $\text{km}^{-2}$  and 46 seals  $\text{km}^{-2}$  ( $\pm 95\%$  CI: 35, 56) for the first survey, and 29 seals  $\text{km}^{-2}$  and 33 seals  $\text{km}^{-2}$  ( $\pm 95\%$  CI: 23, 42) for the second survey for the truncation and decay function methods respectively.

Density values were consistently higher during the first survey than of the second. However, this difference was not significant using the truncation method (ANOVA  $f_{(1,15)} = 2.69$ ,  $p = 0.12$ ) or the decay-curve method (ANOVA  $f_{(1,15)} = 1.81$ ,  $p = 0.20$ ) and so it was considered reasonable to give a combined density estimate. Using the arithmetic mean, this was 39.64 seals  $\text{km}^{-2}$  ( $\pm 95\%$  CI: 30, 49). At this density there would have been 404000 ( $\pm 95\%$  CI: 220000, 530000) seals in the survey area. Table 2.6 shows the density estimates and associated coefficients of variation derived from using the different correction factors described.

### ***Error estimation***

Autocorrelation within transects as well as coherence to previous methods of estimating variance, meant that the coefficient of variation was

estimated using the transect as the sampling unit, this gave final CV's of 7.47% (first survey) and 11.84% (second survey) for the truncation method and 11.26% (first survey) and 13.94% (second survey) for the decay function. It should be noted that though this is a commonly used method, it does not incorporate within transect variability, see discussion.

Non-parametric bootstrapped estimates of variance, based on 1000 iterations with transect density as the sampling unit, gave CV's of 9.21% (first survey) and 12.92% (second survey) for the truncation method and 12.34% (first survey) and 15.35% (second survey) for the decay function; consistent with values obtained from the original eight transects.

**Table 2.6. The density of Antarctic fur seals (seals km<sup>-2</sup>) observed within the Western Core Box to the northwest of South Georgia, January 2001. Means are the arithmetic mean of all transects ( $n$  transects = 8), with transects weighted for effort (see methods). Highlighted cells indicate final density estimates with all corrections where both surveys have been combined.**

Method	Weighted mean ( $D_i$ ) (seals km <sup>-2</sup> )	Lower 95% CI	Upper 95% CI	%CV	Seals in WCB
<b>First survey</b>					
Uncorrected	19.15	14.60	23.70	12.12	204247
Truncated	32.01	26.41	37.61	8.71	341401
Decay curve	33.18	25.52	40.84	11.49	353911
Truncated with sea state	36.54	30.15	42.93	8.92	389729
Decay curve with sea state	34.84	26.99	42.69	11.78	371607
Truncated with sea state and dive	42.83	36.56	49.10	7.47	456886
Decay curve with sea state and dive	45.88	35.23	56.53	11.84	489374
<b>Second survey</b>					
Uncorrected	16.48	10.95	22.01	17.12	175823
Truncation	24.28	16.62	31.94	15.86	258949
Decay curve	26.38	19.28	33.48	13.39	281380
Truncated with sea state	27.71	18.97	36.46	16.10	295604
Decay curve with sea state	27.70	20.43	34.97	13.73	295449
Truncated with sea state and dive	29.39	22.90	35.88	11.26	313515
Decay curve with sea state and dive	32.92	23.92	41.92	13.95	351138
<b>Combined surveys</b>					
Uncorrected	17.82	12.78	22.86	14.62	190035
Truncated	28.14	21.51	34.77	12.28	300175
Decay curve	29.78	22.40	37.16	12.44	317645
Truncated with sea state	32.13	24.56	39.69	12.51	342666
Decay curve with sea state	31.27	23.71	38.83	12.75	333528
Truncated with sea state and dive	36.11	29.73	42.49	9.37	385201
Decay curve with sea state and dive	39.40	29.58	49.22	12.90	420256
<b>Overall average</b>	<b>39.64</b>	<b>30.06</b>	<b>49.23</b>	<b>12.64</b>	<b>404461</b>

## **2.4 DISCUSSION**

### ***2.4.1 Estimating the abundance of Antarctic fur seals at sea by line-transect***

This study is the first attempt to quantify the abundance of ottarid seals from at-sea transect surveys. Survey data were adjusted for distance from the observer, environmental survey conditions (sea state) and dive behaviour to realise absolute density estimates within a defined study region. The conspicuousness as well as relative high density of Antarctic fur seals in the waters around South Georgia facilitated this estimate, whilst individual behaviour recorded concurrently by telemetry allowed spatially and temporally accurate behaviour to be considered in density adjustments. The survey techniques and adjustment framework developed here provides an effective methodology for obtaining the at-sea density of Antarctic fur seals in areas of high density.

I estimated an uncorrected density of 190000 seals within the 10640 km<sup>-2</sup> Western Core Box (WCB), however following corrections for distance from the transect line, sea state and dive behaviour this estimate doubled to a final estimate of 404000 (CV = 12.64 %) seals in the WCB during January 2002.

### ***2.4.2 Variance of abundance estimates***

The primary survey design used in this study was developed to provide an estimate of krill density within the study area using ship-based acoustic interrogation along eight long transects. In a similar way to Antarctic fur seals, krill is patchy in its distribution (Mangel, 1994; McClatchie et al., 1994), and thus results in similarly negatively biased and sequentially

autocorrelated data sets. Indeed since krill is the primary prey of Antarctic fur seals around South Georgia it may even be that the distribution of krill drives the distribution of Antarctic fur seals, this would result in similar spatial characteristics. It is important therefore how we describe the sample mean and variance.

Possibly the most accurate way to describe the variance of the sample is at the finest resolution possible, in this study, five-minute periods along the transect, or in the case of the krill data each acoustic interval or even a ping by ping resolution. However, the patchy nature of both populations has the effect that these fine-scale sampling units are serially autocorrelated and cannot be treated as independent.

The next logical stage is to pool these fine scale sampling units to the scale at which sampling units are sufficiently large to render unimportant any serial autocorrelation within the transect. This would work where the study area had no natural gradient. In this study however, where transects are aligned perpendicular to depth isobaths, and as both seal and krill distributions can be related to the depth gradient, there is a second level of autocorrelation which is present over the entire transect length, i.e. two inshore segments are likely to be more similar than a inshore and offshore segment.

Samples do however, become independent when the transect is the sampling unit. This has the cost of reducing the sample size to  $n = 8$  in each survey. Because transects are independent, it is possible to produce robust estimates of mean density with associated variance, by doing, so this effectively bases the estimation of variance on the standard error not on the

standard deviation. This is the most common method used to describe variance in line-transect surveys (Jolly & Hampton, 1990a, b) and is also the method integrated into such packages as DISTANCE (Buckland et al., 1993b). In addition non-parametric bootstrapping of the density values of each transect, generated very similar variance estimates providing additional support to the variance estimates. These values however, not incorporating variance from within the transect, should still be considered underestimates.

### ***2.4.3 Accounting for animals present but not detected***

#### ***Observer fatigue***

Observer experience and ability can influence the numbers of animals sighted (Vandermeer & Camphuysen, 1996). As this was a single platform survey, i.e. only one team of observers, no comparison between observers and hence measurement of observer error, was possible. However, based on mean density and sample variance, there was no evidence of observer fatigue over the duration of each surveyed transect.

#### ***Distance from the observer***

This study was restricted to Antarctic fur seals however all species of bird and mammal observed were recorded. This multi-species approach, and the high density of predators around South Georgia, meant that attempts to record distance and angle to each individual or cluster was not possible within the scope of this study. Moreover, it was not appropriate to assume complete detection of Antarctic fur seals across a 300 m fixed width transect. Therefore, the combined approach of pooling the distance of observations into four distance bands, allowed both line-transect and strip-transect analysis methods to be used. This pooling method is popular with respect to at-sea

surveys of seabirds, the densities and patchy distribution of which are probably more similar to Antarctic fur seals than are other marine mammals (Buckland & Borchers, 1993; Tasker et al., 1984).

Both approaches suggested that the detection probability declined severely beyond 100 m from the observer and gave very similar density estimates. In this study it was clear that, this was quite different to the 300 m chosen as a truncation distance for surveys of Northern fur seals (*Callorhinus ursinus*) (Buckland et al., 1993a).

#### ***Adjustments for sea state***

Sea state had influence on the estimated seal density (mean increase 10.6%). Due to low sampling effort in sea states zero and one, it was only possible to adjust to sea state two rather than the ideal sea state zero conditions. Studies of cetaceans have found little but some reduction in detection probability between sea state two and zero (Macleod et al., 2003). No white caps are seen at sea state two, and though this will have had a slight negative bias on density estimates, the major reduction in detection probability occurred at sea state three or greater. Typical rough seas around South Georgia make it unlikely that a survey could be completed in idealized survey conditions.

#### ***Adjustments for diving animals***

Combined satellite and time depth recorder studies on lactating female Antarctic fur seals (Staniland & Boyd, 2003), have shown diving behaviour to have both a spatially specific and diurnal component such that, during the day and hence during the time of this survey, animals dive for longer and with greater frequency when over the continental shelf than when off it. Since



transects were aligned perpendicular to the continental shelf break, there was a potential to miss more seals over the shelf than off. This spatially specific behaviour highlights the need to consider animal behaviour even where only indices of relative abundance are required as much as in studies of absolute abundance.

In this study diving behaviour specific to the survey area and time of survey was found to have some influence on the detectability of seals, and was estimated to reduce the number of seals observed by 14%. This model required the assumption that animals remained stationary once sighted.

Sensitivity analysis showed the model to be most sensitive to the total proportion of time spent diving ( $T_d$ ) rather than parameters describing observation period ( $t$ ) or dive duration ( $u$ ). In this study it was not possible to accurately calculate forward detectability from the observer, and hence it was difficult to estimate  $t$ . It was therefore assumed that it was similar to the sideways reduction in detection probability; it would be useful to measure this in future surveys.

Animals may swim horizontally whilst underwater, and could move out of the survey strip. This will of course be a flux and animals will also be able to move underwater into the strip. In this survey it is possible that where a seal was sighted, dives and was sighted again, it may be counted twice. This is only likely to be a serious problem where an animal is diving so long that the observer loses track of the animal's location. This will most likely occur when an animal is foraging and hence diving for extended periods, but just shorter than the length that a point on the water's surface is under observation.

All these factors may have a slight influence on the number of animals detected. Overall however they are unlikely to have any significant effect; there seem to be as many potential small positive as there are negative biases, and the confidence intervals around the final estimates should more than allow for any of these factors.

### ***Other factors influencing detection probability***

There are a large number of potential factors influencing detectability. The two main ones not fully investigated in this study are behavioural response to the vessel (Palka & Hammond, 2001; Turnock & Quinn, 1991) and observer error (Vandermeer & Camphuysen, 1996).

Movement of animals in response to the vessel is a problem common to many transect surveys, with animals attracted to, or repelled from, the vessel causing a large potential bias (Barlow, 1995; Palka & Hammond, 2001; Turnock & Quinn, 1991). Without aerial survey or a second survey platform, it is not possible to fully determine larger-scale vessel responses. Within the survey range vessel response can be investigated by looking for certain characteristic shapes in the distribution curves away from the transect line and by recording animal behaviour at first sight.

The DISTANCE decay curves showed only small and inconsistent evidence of ship avoidance. This was only found for the second survey and was indicated by the lower detection rate in the 0-50 m band than that for 51-100 m. With this only occurring for one survey and the curves fit limited to four distance bands it is probably unnecessary to place too much emphasis on this. Animal swimming behaviour and direction was recorded at first sight, as well as any significant change. The only visible response behaviour to the

vessel was where seals moved to avoid direct contact with the ship. At-sea surveys of northern fur seals (Buckland et al., 1993a) also found no evidence of vessel attraction. If vessel avoidance did take place it was not severe, and must only have only happened with a small portion of the population. There is recent evidence of Antarctic fur seals occurring as bycatch in fisheries for krill and of them learning to take fish from the lines of long-line fishing boats (South Georgia Fisheries Officer (Katherine Ross), Pers. Com.). Such an attractive force could potentially modify behaviour in future.

#### ***2.4.4 Validation of density estimates***

It is important to know, but difficult to assess, whether the abundance estimates found in this study are valid. There have been no prior attempts at estimating the at-sea density of Antarctic fur seals around South Georgia, however, Boyd et al. (2002), created a simple empirical model of the distribution of lactating female Antarctic fur seals around South Georgia based on satellite telemetry tracking of individual seals. They generated a probability density surface of seals around the island. By scaling this up to the estimated population size, it has been possible to create an independent estimate of the density of seals within the survey area.

The model used tracks of centrally placed foraging female Antarctic fur seals, and their dive behaviour, recorded from two locations on South Georgia, namely Bird Island and Husvik, Stromness Bay. The model then described the shape of a typical foraging event from the central point, the site of the offspring. This was best described by the distance and angle travelled from the colony. The model explained 42% and 53% of the variance of observed distribution for the two sites respectively. This function was then

applied to all the colony sites on South Georgia, as described by Boyd (1993), to create an estimate of the distribution of foraging by lactating female Antarctic fur seals as a probability density function around the whole Island. By scaling up this function to the estimated population size (Barlow et al., 2002), This density distribution was used to estimate the number of seals present in the WCB. A more detailed description of this model can be found in Appendix One.

By scaling the model of foraging distribution for lactating female Antarctic fur seals as described by Boyd et.al. (2002), to a estimated all age population size of 3.5 million (Barlow et al., 2002; Boyd, 1993), the estimated density of seals within the study area is 30 seals km<sup>-2</sup>, equivalent to 316000. This estimate is well within the 95% confidence interval of the density estimate from line-transects. This population estimate is from the early 1990s since which time the population has increased (Barlow et al., 2002; Boyd, 1993; Reid & Forcada, 2005). The model distribution was only based on lactating females (i.e. not all age classes as included in this study). It therefore is likely that a comparison based on a current estimate of the population may yield a value even closer to, or possibly greater than the estimate from this study.

#### ***2.4.5 Using line-transect survey methods for future surveys of seal abundance at sea***

This study has shown that line transect methods are suited to estimating the abundance of seals in a specific area. However, the application of these methods are species and area specific and it may be that the high

densities and highly conspicuous nature of Antarctic fur seals provides a suitability that may not be applicable to the species or regions.

At South Georgia the density of seals at sea is very high. This limited the survey methods to grouping observations into perpendicular distance bands and five-minute observation periods along the transect (~1.6 km intervals). Where population densities are lower the survey would be much improved by recording the angle and distance to each individual or group sighted. It would also be of great value to record individual group size, as the size of different groups can greatly affect detectability. In this survey Antarctic fur seals were often seen in large groups, with 87% of observations including more than one seal, this was unlike observations in surveys of Northern fur seals, where only 9% of observations included more than one animal (Buckland et al., 1993a).

This study found that seal detectability decreased rapidly beyond 100 m from the observer, and it may be that future surveys would benefit from restricting the search area to a 100 x 100 search box. The benefit of the 300 m forward distance from the observer was however particularly beneficial in the interpretation of the influence of diving, as if the forward observation period were only 100 m the ratio of  $t/u$  would be much reduced and the potential for missing diving animals greatly increased. Seeing less animals is not a difficulty providing the number of animals missed can be accurately assessed. However where a survey observes very few animals, or has a lower survey effort (as is the case with reducing the search area) then the ability to accurately assess detection probabilities may be compromised. With these factors in mind the optimal search area in regions of high density may be a

100 m wide strip transect, with records made of the forward distance from the observer, possibly into distance bands up to 300 m ahead of the ship. There would also be great benefit in comparison with surveys from other survey platforms such as aircraft or a yacht, where the response of predators to the survey vessel may be very different.

This study was unique in that concurrent individual behavioural data were available. Whilst the use of behavioural data from the literature would no doubt go a long way to improving density estimates, having spatially and temporally specific data was of great benefit. Other studies should consider the potential of fine scale behaviour on the abundance and distribution of animals observed.



## CHAPTER THREE

### **The density and distribution of gentoo penguins, macaroni penguins and prions to the northwest of South Georgia, January 2002**

#### **3.1 INTRODUCTION**

Whilst the primary focus of this thesis is on the distribution and density of Antarctic fur seals at South Georgia, understanding of this can only be put into perspective with an understanding of the distribution and density of other principle krill consumers in the region.

Current CCAMLR krill management schemes consider Antarctic fur seals and macaroni penguins as the most significant krill predators (Hewitt et al. 2004c). Other species taking a significant proportion of the krill biomass are gentoo penguins (*Pygoscelis papua*), estimated by Croxall et al. (1984) to consume 61000 tonnes of krill per year in the South Georgia area, fish (Kock 1985) and baleen whales (Reilly et al. 2004). Despite their small individual mass Antarctic prions (*Pachyptila desolata*), were estimated by Croxall et al. (1984) to consume 1345000 tonnes of krill per year, half that estimated by the same study for macaroni penguins (3872000 tonnes krill year<sup>-1</sup>). The line-transect survey methods used within this study were not suited to robust estimates of cetacean density, and were not estimated.



This chapter uses the methods developed in Chapter Two to estimate the density and distribution of macaroni penguins, gentoo penguins and prions to the northwest of South Georgia, using data gathered during the multi-disciplinary cruise carried out in January 2002.

## **3.2 METHODS**

All data were collected between January 13<sup>th</sup> and 28<sup>th</sup> 2002 from the RRS James Clark Ross, in the long-term study area to the northwest of South Georgia, from here on called the Western Core Box (WCB), Figure 2.1.

The survey consisted of eight, parallel, 80 km transects, within a study box measuring 80 by 120 km. The whole survey was repeated twice with a minimum of seven days between the surveying of replicate transects. Animals on the water were recorded into distance bands perpendicular to the transect line. Flying birds were recorded as a snapshot every minute, and were not recorded into the distance bands that were used for birds on the water surface. We assumed complete detection probability for birds counted by the snap shot method (Tasker et al. 1984; Tasker et al. 1985; Van Franeker 1994).

Where results are used in the construction of correction factors they are included within these methods. The results of the application of these correction factors are dealt with solely in the results (Section 3.3).

### ***3.2.1 Adjusting for animals present but not detected***

The number of animals observed is likely to be only a fraction of the numbers of animals actually present. In this study, the number of animals

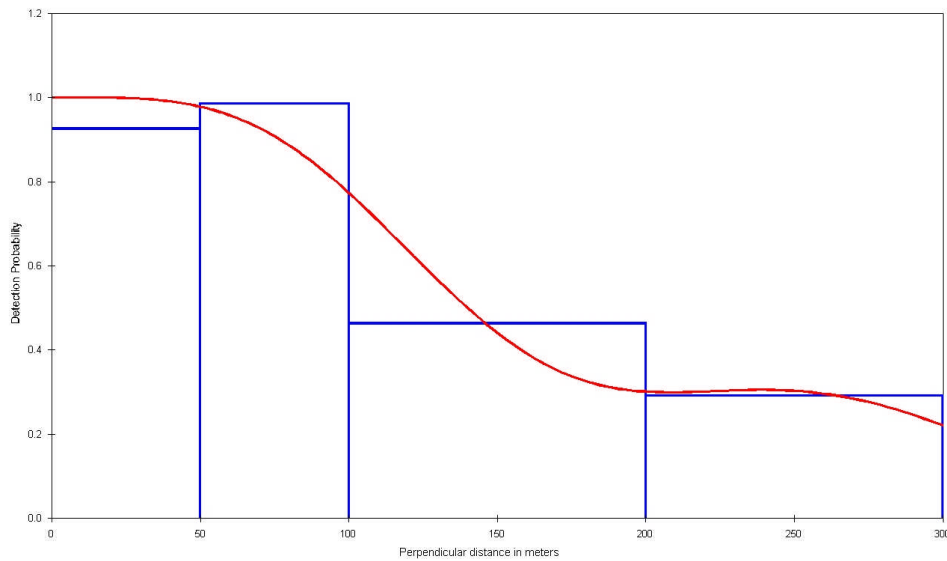
observed is adjusted to allow for the effects on detection probability of distance from the observer, sea state, and, for penguins, time spent diving. These scalars were estimated and applied following procedures outlined in Chapter Two, and this should be referred to for detailed methodologies. How these methods relate to the specific species considered here is as follows:

***Accounting for distance from observer***

It was expected that the probability of detecting a bird would decrease with increasing distance from the observer; this was investigated using the software package DISTANCE (Buckland et al. 1993a). The number of penguins observed was quite small and so I have made the assumption that the influence of distance from observer on detection probability would be similar for both species. Observations of macaroni and gentoo penguins were therefore combined prior to DISTANCE analysis. Following the model selection procedures outlined in Chapter Two, for both prions and penguins the final DISTANCE model selected was half-normal with cosine adjustments.

$$\text{Half-normal model} = \exp(-y^2 / 2\sigma^2) \quad \text{Equation 3.1}$$

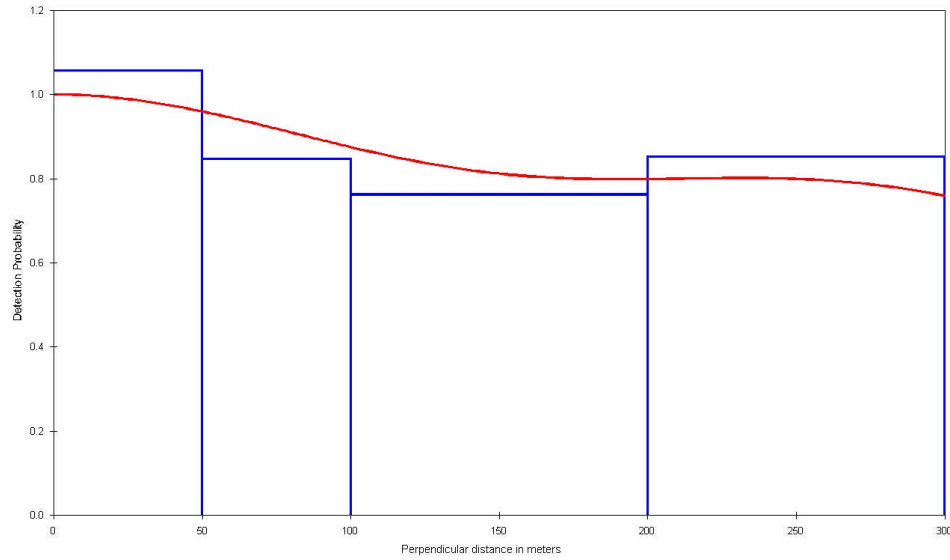
$$\text{Cosine series expansion} = \sum_{j=2}^m a_j \cos\left(\frac{j\pi y}{w}\right) \quad \text{Equation 3.2}$$



**Figure 3.1.** Sightings distribution of macaroni and gentoo penguins against perpendicular distance from the observer for both surveys combined. The data were fitted with a half-normal function; with cosine adjustment parameters. The curve fitted indicates the estimated detection probability.  $n = 229$ ,  $p = 0.56$ ,  $\pm 95$  CI 0.42, 0.76;  $f(0) = 0.0058 \pm 95\%$  CI 0.0043, 0.0078.

The half-normal model formed a good fit with penguin sighting distributions and showed their detectability to be heavily influenced by distance from the observer, with a detection probability of  $p = 0.56$  ( $\pm 95\%$  CI 0.42, 0.76).

The prion fit to the decay models was not so good, with more animals being sighted in the furthest distance band (201-300 m) than in the central distance band (101-200 m). There were however more animals sighted in the first distance band than those further away and distance from the observer was considered to have some influence on the number of animals sighted. Application of the half-normal model gave detection probability as  $p = 0.85$  ( $\pm 95\%$  CI 0.72, 1).



**Figure 3.2. Sightings distribution of prions against perpendicular distance from the observer for both surveys combined. The data were fitted with a half-normal function; with cosine adjustment parameters. The curve fitted indicates the estimated detection probability.  $n = 1103$ ,  $p = 0.85$ ,  $\pm 95$  CI 0.72, 1;  $f(0) = 0.0038 \pm 95\%$  CI 0.0033, 0.0046.**

To be consistent with other variables to be adjusted for, the detection probability was applied as a multiplier to the whole data set. This was applied as:

$$D_a = \frac{D_u}{p} \quad \text{Equation 3.3}$$

Where  $D_a$  = the adjusted density,  $D_u$  = the unadjusted density (of animals sighted on the waters surface) and  $p$  = the probability of detection.

*Accounting for sea state*

Sea state zero was not experienced during the survey and only a very small number of observations were made during periods of sea state one. A correction factor to adjust the observation data to a notional sea state two, was generated where:

$$\text{Correction factor} = \frac{\overline{B}_{3,4,5}}{\overline{B}_2} \quad \text{Equation 3.4}$$

and  $B_i$  is the Beaufort sea state.

The detectability of smaller penguins decreased significantly between sea state two and greater than sea state two (Mann-Whitney U test,  $W = 235318$  ( $n = 290, 1266$ ),  $p = <0.001$ ). There was however a small number ( $n = 6$ ) of observation periods with very high counts that were observed in sea state five, these observations biased measures of the influence of sea state. For this reason, observation periods with a count greater than the 99<sup>th</sup> percentile were removed from subsequent sea state analysis and were not adjusted according to their sea state.

There was no significant difference (Kruskal Wallis,  $H_{(320, 1268)} = 14.88$ ,  $p = <0.001$ ) between the densities of animals observed in sea states 3, 4 or 5, and so the arithmetic mean of these values was used for the correction factor.

With prions there was no discernable influence of sea state on the numbers of animals observed between observations made in sea state two and sea states three to five (Mann-Whitney U test,  $W = 53597$  ( $n = 143, 643$ ),  $p = 0.47$ ) and so no subsequent adjustments were made.

**Table 3.1. Densities of macaroni and gentoo penguins sighted under different Beaufort sea state conditions and correction factors used to adjust sightings of sea states >2 to notional Beaufort sea state 2.  $n$  is the number of observation periods and mean is the arithmetic mean animal density within each period (animals km<sup>-2</sup>). See text for methods.**

Sea state	$n$	Mean	$\pm$ 95% CI	Scaling probability
Sea state 2	320	0.764	0.45, 1.08	0.28
Sea state 3 – 5	1268	0.220	0.14, 0.39	

### *Accounting for diving animals*

As with Antarctic fur seals in Chapter Two it was assumed that some penguins may be below the surface at the time that observations are made and would hence would go unobserved. Following the procedures laid out in Chapter Two the influence of diving on detection probability was assessed using a Monte Carlo simulation model (Manly, 1991) around the general framework:

$$P = (T_s p_s) + (T_d p_d) \quad \text{Equation 3.5}$$

Where  $P$  = overall the probability of sighting an animal,  $T_s, d$  = the proportion of time spent at the surface or diving respectively, and  $p_s, d$  is the probability of detecting an animal that is either at the surface or diving respectively.  $p_s$  was assumed to be equal to one, and  $p_d$  is calculated as:

$$p_d = \frac{t}{u} \quad \text{Equation 3.6}$$

Where  $u$  = the average dive duration and  $t$  = the period of time during which a point on the water surface is within the visual range of the observer.

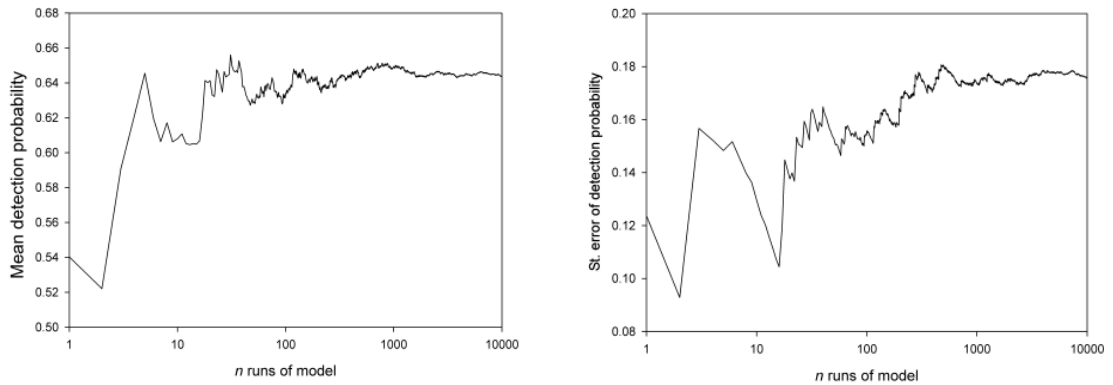
The parameter  $t$  was based upon the frequency distribution of observation periods with a detection probability equal to one, and was estimated in the same way as described in Chapter Two. Parameters

describing macaroni and gentoo penguin dive behaviours were taken from the literature and were deemed to be appropriate to the time of the survey, these are shown in Table 3.2. (Williams et al. 1992; Croxall 1993; Trathan and Croxall 2004). The only major difference in model parameters between these two species was average dive duration. Average gentoo penguin dive duration was approximately 34% longer than that for macaroni penguins. The total proportion of time spent diving ( $u$ ) was similar for both species and the observation period ( $t$ ) was exactly the same.

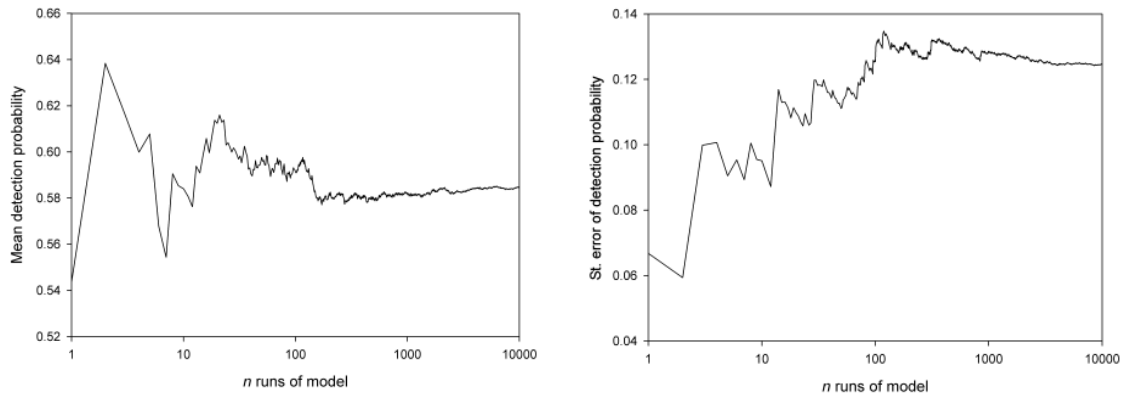
**Table 3.2. Dive model parameters for macaroni and gentoo penguins. Values are specific to South Georgia, with animals at the same period of their annual cycle.**

Parameter	Mean	SD	Source
<b>Macaroni penguins</b>			
$T_s$	0.480	0.079	Croxall et al. (1993)
$T$	24.44	17.63	See Chapter Two
$U$	83.15	40.30	Trathan & Croxall (2004)
<b>Gentoo penguins</b>			
$T_s$	0.484	0.12	Williams et al. (1992)
$T$	24.44	17.63	See Chapter Two
$U$	126.23	19.50	Williams et al. (1992)

Both models and their associated standard errors stabilised near to 1000 runs of the model (See Figures 3.3 and 3.4). When run over 10000 iterations the model found detection probability as a result of dive behaviour to be 0.644 (SE 0.18) for macaroni penguins and 0.586 (SE 0.13) for gentoo penguins.



**Figure 3.3. Results of the macaroni penguin dive model showing the influence of diving on detection probability and its associated standard error averaged over 1 to 10000 runs of the model.**



**Figure 3.4. Results of the gentoo penguin dive model showing the influence of diving on detection probability and its associated standard error averaged over 1 to 10000 runs of the model.**

### *Sensitivity analysis*

As dive models for both species had the same structure and their parameters had similar error distributions sensitivity of the model was only assessed for the macaroni penguin based model. Sensitivity analysis was carried out by systematically incorporating uncertainty belonging to each variable ( $T_s$ ,  $t$ , and  $u$ ), whilst holding the others constant at their deterministic values and assessing the proportion of the total variance attributable to the unrestricted variable. Also investigated was the effect of independently varying each of the deterministic input variables on the final output value. To



do this the average value of the input variable was increased by 10% whilst maintaining other components constant at their deterministic values.

**Table 3.3. Variation in detection probability of macaroni penguins associated with each variable, when present in the model as the only variable with uncertainty, expressed as a proportion of the total variance in detection probability. Also shown is the sensitivity of detection probability to a 10% change in the average value of the input variables. A negative value indicates when the change in detection probability was opposite to the direction of change in the value of the variable.  $n$  iterations of model = 1000. See text for methods.**

Variable in which uncertainty was incorporated	% CV	Proportion of total variance explained	Sensitivity ( $\Delta\%$ )
Proportion of time spent at surface ( $T_s$ )	16.44	0.18	5.96
Observation duration ( $t$ )	72.11	0.36	2.69
Dive duration ( $u$ )	48.47	0.46	-2.41

Accounting for only 18% of the overall variance, sensitivity analysis revealed the model to be insensitive, being most sensitive to the total proportion of time spent at the surface ( $T_s$ ), with a 10% change in  $T_s$  resulting in a 5.96% change in the final value. Observation duration ( $t$ ) and dive duration ( $u$ ) both had higher influence on total variance (0.36 and 0.46 respectively), but a 10% change in these values had a lower influence on the resulting probability, (2.69 and -2.41% respectively).

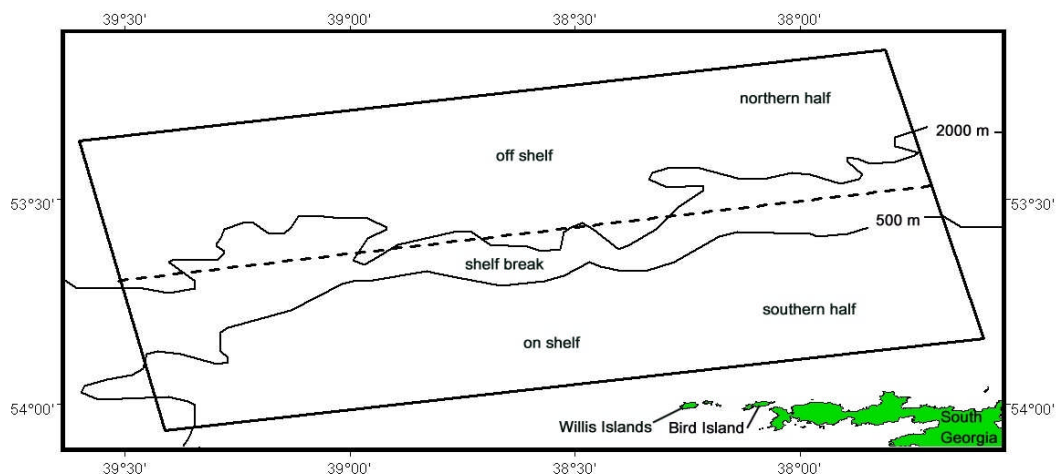
### ***3.2.2 Describing distribution***

#### ***Region specific density***

Whilst a single density value for a region has great value, animals are rarely equally distributed and a density value may represent a higher localised density surrounded by a desert of much lower densities. For this reason it is essential to also consider localised densities and the distribution of predators

within the WCB. This was done by dividing the WCB into sub-regions as well as by mapping the distribution of predators along transects.

Predator densities were examined in the northern and southern sectors of the WCB, and in regions divided by depth, these were: on-shelf (shallower than 500 m), shelf break (500 – 2000 m deep) and off-shelf region (deeper than 2000 m), see Figure 3.5. These regions were thought to best represent the different underlying physical characteristics of the region, which are thought to subsequently influence predator distribution (Murphy et al. 1997; Trathan et al. 1998b; Staniland and Boyd 2003; Staniland et al. 2004; Tanton et al. 2004).



**Figure 3.5.** Map showing Western Core Box study area with spatial divisions based on depth (0 - 500 m, 500 – 2000 m and deeper than 2000 m) and northern and southern sectors of the area. Also shown are Bird Island and the Willis Islands.

### *Mapping distribution*

The distribution of predators along transects was visualised by mapping the density of animals within each 5-minute observation period as a proportion of the sum of density within that survey. Maps were generated using ArcView 3.2 GIS software (Environmental Systems Research Institute Inc., 1992-1999).

### 3.3 RESULTS

#### 3.3.1 Overall predator density

##### *Penguins*

Macaroni and gentoo penguins were sighted in only 6.1 and 6.7% of all observation periods respectively. The uncorrected mean density of macaroni and gentoo penguins, averaged between the first and second surveys, were similar, being 1.09 ( $\pm$  95% CI 0.66, 1.52) and 1.07 ( $\pm$  95% CI 0.64, 1.50) birds km<sup>-2</sup> respectively. Correcting these estimates for distance from the observer increased the estimates by 78% for both species. Adjusting for animals missed due to higher sea states, increased these estimates by 43% and 40% for macaroni, and gentoo penguins respectively and increases to compensate for dive behaviour were 132% and 150% for macaroni and gentoo penguins respectively. This gave final, adjusted, density estimates of 4.39 ( $\pm$  95% CI 1.95, 7.72) for macaroni penguins km<sup>-2</sup>, and 4.64 ( $\pm$  95% CI 2.13, 8.11) for gentoo penguins km<sup>-2</sup> (see Tables 3.4 and 3.5).

##### *Prions*

The percentage of observation periods where prions were sighted, 35%, was much higher than that for penguins. 65% of all prion observation records were for flying birds. The unadjusted density of prions, averaged between surveys was 25.44 ( $\pm$  95% CI 13.16, 37.72) prions km<sup>-2</sup>. The number of prions observed was not influenced by sea state. Prions are surface feeders rarely diving beneath the waters surface (Prince 1980; Prince and Morgan 1987; Goss et al. 1997; Reid et al. 1997a; Cherel et al. 2002). For this reason no adjustment was made for diving. The only adjustment to the observed

densities of prions was for distance from the observer, and this was only applied to the birds on the waters surface. Adjusting observations for distance from the observer resulted in an 6% increase in density such that the final density value, averaged between surveys was 27.01 ( $\pm$  95% CI 13.97, 40.05) prions km<sup>-2</sup>, Table 3.6.

### ***Differences between surveys***

For both species of penguin, the density of birds observed was slightly higher during the second survey, but this difference was not significant (Kruskal-Wallis,  $n = 794$ ,  $H = 1.09$ ,  $p = >0.05$  for both penguin species). For prions there was a greater density of birds observed during the second survey, but again this was not significant (Kruskal-Wallis,  $n = 794$ ,  $H = 1.12$ ,  $p = >0.05$ ).

#### ***3.3.2 Predator distribution***

The distribution of macaroni and gentoo penguins was very much on-shelf. This pattern was particularly pronounced for gentoo penguins with very few penguins sighted beyond the shelf break region. Macaroni penguins were sighted more in the northern sector of the box, than gentoo penguins. Within the 200 m isobath both species of penguin were seen fairly regularly, particularly to the north of the South Georgia, at the eastern end of the WCB.

Prions appeared to travel slightly further than penguins, and though density was still very much higher on-shelf, they were found in all regions of the WCB. Inshore density was highest around the 200 m depth contour, particularly along transects 3.2 and 4.1. Interestingly, the distinct regions were used consistently between the first and second surveys.

**Table 3.4. Macaroni penguin density in the WCB, January 2002.**

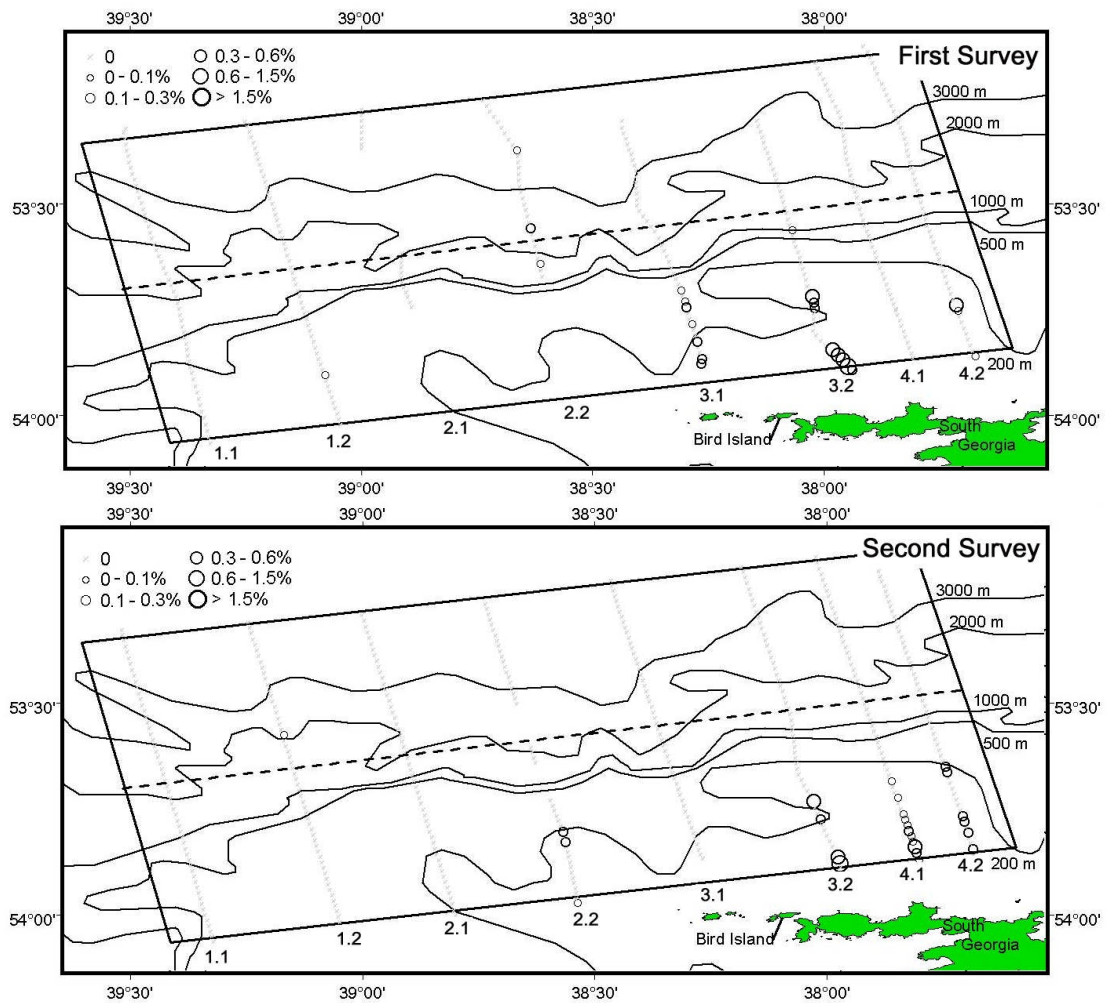
<b>Area</b>	<b>Density (birds km<sup>-2</sup>)</b>	<b>%CV</b>	<b>± 95% CI</b>	<b>In area (individuals)</b>
<b>First Survey</b>				
Whole box	5.21	24.59	2.68, 7.72	55434
On-shelf	9.45	32.69	4.89, 14.03	38331
Shelf break	0.00	-	-	0
Off-shelf	0.22	2.16	0, 0.66	998
Southern Box	8.28	30.75	4.25, 12.31	44050
Northern Box	0.15	1.80	0, 0.56	798
<b>Second Survey</b>				
Whole box	3.56	17.17	1.94, 5.19	37878
On-shelf	6.41	22.63	3.53, 9.29	26000
Shelf break	0.00	-	-	0
Off-shelf	0.00	-	-	0
Southern Box	5.71	21.56	3.14, 8.29	30377
Northern Box	0.00	0.00	-	0
<b>Combined</b>				
Whole box	4.39	20.88	1.94, 7.72	46656
On-shelf	7.93	27.66	3.53, 14.03	32166
Shelf break	0.00	-	-	0
Off-shelf	0.11	1.08	0, 0.66	499
Southern Box	7.00	26.16	3.14, 12.31	37213
Northern Box	0.08	0.90	0, 0.17	399

**Table 3.5. Gentoo penguin density in the WCB, January 2002.**

<b>Area</b>	<b>Density (birds km<sup>-2</sup>)</b>	<b>%CV</b>	<b>± 95% CI</b>	<b>In area (individuals)</b>
<b>First Survey</b>				
Whole box	5.35	26.77	2.58, 8.11	56924
On-shelf	9.80	35.69	4.80, 14.80	39751
Shelf break	0.00	-	-	0
Off-shelf	0.00	-	-	0
Southern Box	8.59	33.55	4.19, 12.99	45699
Northern Box	0.00	-	-	0
<b>Second Survey</b>				
Whole box	3.92	18.87	2.13, 5.71	41709
On-shelf	7.04	24.87	3.88, 10.20	28556
Shelf break	0.00	-	-	0
Off-shelf	0.00	-	-	0
Southern Box	6.28	23.59	3.45, 9.12	33410
Northern Box	0.00	0.00	-	0
<b>Combined</b>				
Whole box	4.64	22.82	2.13, 8.11	49316
On-shelf	8.42	30.28	3.88, 14.80	34153
Shelf break	0.00	-	-	0
Off-shelf	0.00	-	-	0
Southern Box	7.44	28.57	3.45, 12.99	39554
Northern Box	0.00	0.00	-	0

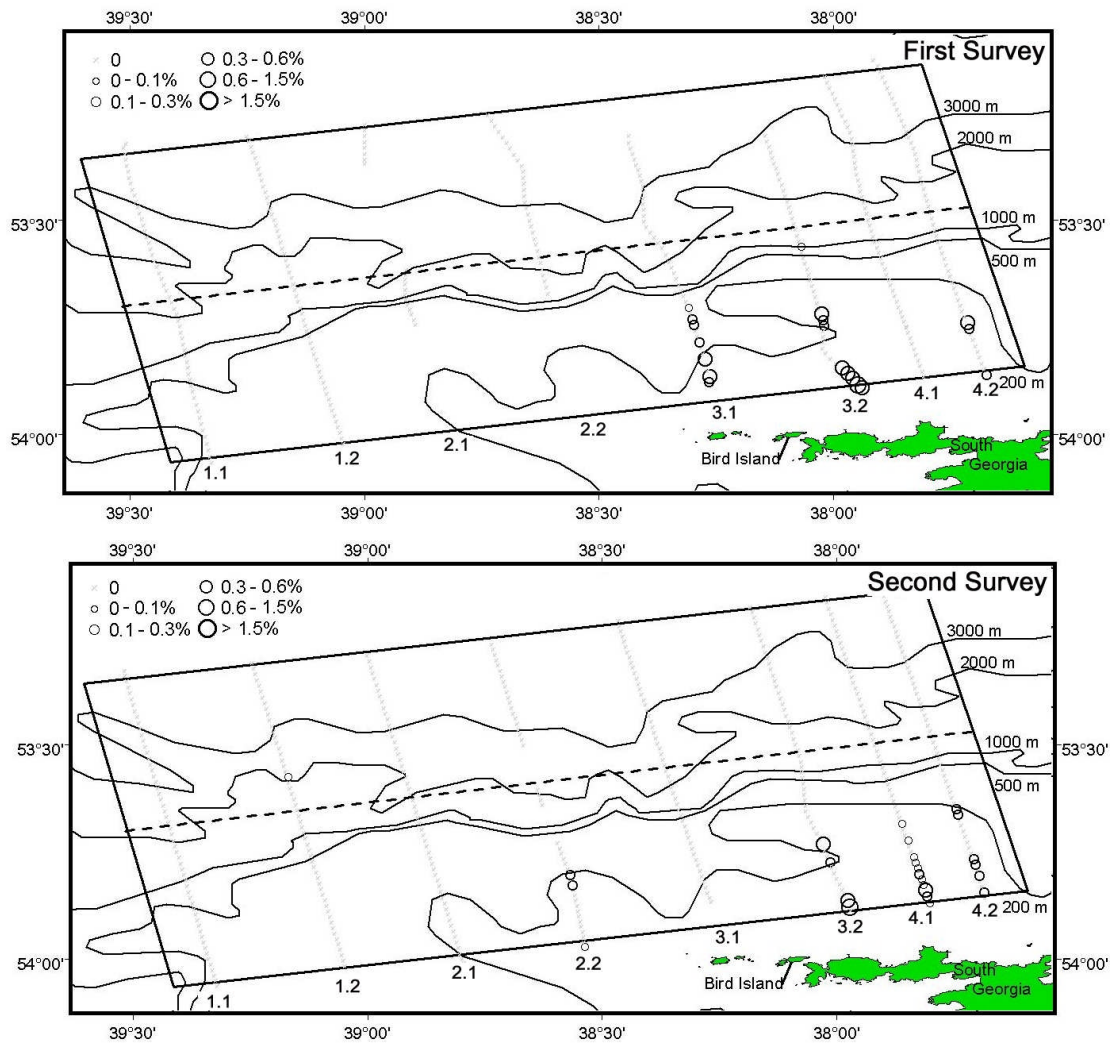
**Table 3.6. Prion density in the WCB, January 2002.**

<b>First Survey</b>				
<b>Area</b>	<b>Density (birds km<sup>-2</sup>)</b>	<b>%CV</b>	<b>±95% CI</b>	<b>In area (individuals)</b>
Whole box	23.98	56.13	7.1, 40.85	255147
On-shelf	42.42	51.84	11.68, 73.16	172064
Shelf break	1.74	30.01	0.49, 2.98	3607
Off-shelf	1.73	32.10	0.60, 2.87	7850
Southern Box	37.32	52.80	10.34, 64.30	198542
Northern Box	1.86	28.24	0.88, 2.85	9895
<b>Second Survey</b>				
Whole box	29.58	32.21	10.13, 49.03	314731
On-shelf	51.54	53.04	16.70, 86.38	209057
Shelf break	2.26	41.91	0.12, 4.41	4685
Off-shelf	1.99	26.70	0.99, 2.97	9029
Southern Box	45.99	33.87	14.89, 77.09	244667
Northern Box	2.43	28.97	1.21, 3.66	12928
<b>Combined</b>				
Whole box	27.01	69.09	13.97, 40.05	287386
On-shelf	47.04	52.80	23.89, 70.90	190804
Shelf break	2.01	38.48	0.75, 3.27	4167
Off-shelf	1.87	28.98	1.13, 2.61	8485
Southern Box	42.01	56.14	21.18, 62.84	223493
Northern Box	2.17	32.23	1.37, 2.97	11544

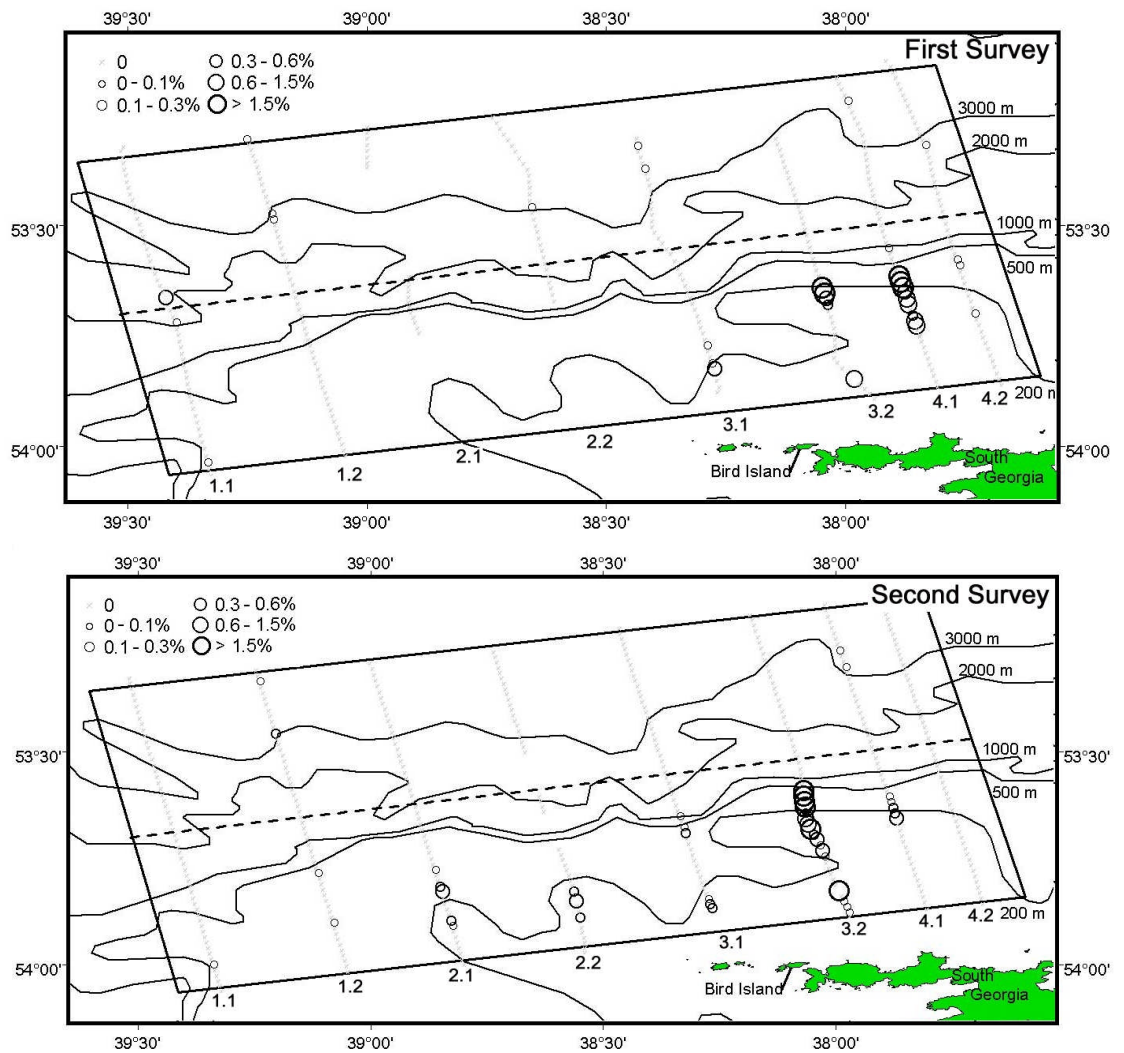


**Figure 3.6.** Map showing macaroni penguin distribution as a percentage of the total cumulative density, for the first and second survey. Crosses indicate survey periods with no penguins observed. Also shown are the 200, 500, 1000, 2000 and 3000 m depth isobaths.





**Figure 3.7.** Map showing gentoo penguin distribution as a percentage of the total cumulative density, for the first and second survey. Crosses indicate survey periods with no penguins observed. Also shown are the 200, 500, 1000, 2000 and 3000 m depth isobaths.



**Figure 3.8.** Map showing prion distribution as a percentage of the total cumulative density, for the first and second survey. Crosses indicate survey periods with no prions observed. Also shown are the 200, 500, 1000, 2000 and 3000 m depth isobaths.

### 3.4 DISCUSSION

#### *3.4.1 Penguin observability and densities*

Penguins sit high in the water, but are small so that the target visible to the observer is small and is also mostly black. These characteristics make them difficult to spot at sea. Penguins were only sighted in ~6.3% of observation periods, with a very similar number of macaroni and gentoo penguins being sighted. The overall increase from unadjusted densities to densities with all corrections applied was 302%, to give final densities of 4.39 penguins km<sup>-2</sup> for macaroni penguins and 334%, to give 4.64 penguins km<sup>-2</sup> for gentoo penguins.

At South Georgia however the population size of macaroni penguins, five million breeding pairs (Trathan et al. 1998b) is much greater than that for gentoo penguins, 90,000 breeding pairs (Williams 1995; Trathan et al. 1996b). It should be noted that the macaroni penguin population size is currently in review and may be considerably smaller than previous estimates (Trathan 2004). Even with a reduction in estimates of macaroni penguin population size, it seems unlikely that the two species should have such similar densities at sea.

There are no baseline density's with which to compare the results of this survey. However, Hunt et al. (1986, 1992) surveyed macaroni penguins in the region, and estimated relative abundances as birds km<sup>-1</sup> along the transect line. The survey used a 300 m width strip transect similar to that used in this survey. Though scaling the values of Hunt's study, using the same methods

applied to our data is crude, it does give some insight into whether the numbers of animals observed within the two studies are comparable.

Hunt's survey was based on 38 radial transects, up to 118 km in length. Transects were based with the centre point at the Willis Isles, to the west of Bird Island (See Figure 3.5). Hunt et al. (1986, 1992) gave relative abundance values within subsections of his total survey region. Two of these sections, when put together, approximately represented the area of the WCB. Adjusting the number of animals sighted along the transect to give an uncorrected density, gave a density of 6.16 penguins km<sup>-2</sup>, if this density is subjected to the same adjustments derived for this study, this would give 61.06 penguins km<sup>-2</sup>. The variance associated with Hunt's density is not available but it is clear that they sighted many more macaroni penguins than this survey. There were however differences in methods between this survey and that of Hunt et al. (1986) having a dedicated observer for penguins. It would be interesting to survey for penguins with a dedicated observer or from a different type of vessel.

There is little evidence in curves describing the decrease in detection probability from observer (Figure 3.1) that penguins were much harder to sight than Antarctic fur seals (Figure 2.7). However, it seems that the survey methods used in this study are not well suited to the smaller penguins. The single-platform observer methods used to collect data during this study did not allow us to estimate  $g(0)$  or perception bias and so it is impossible to test the assumption that all animals on the transect line were sighted. In the northern hemisphere similar survey methods have been applied to at-sea

surveys of guillemots (*Uria aalge*) and razorbills (*Alca torda*) (Taylor and Reid 2001). These authors did not report any difficulties with surveying birds, which though they may have shorter dive durations, may have detection probabilities similar to small penguins. For their survey, Taylor & Reid (2001) used a correction factor of 1.6, effectively the same as a percentage increase of just 60%. Though alcids on the waters surface probably have similar detectability to penguins, many of Taylor & Reid's observations may have been of flying birds. Our results in this study illustrate the high detectability of flying birds in contrast to that on the waters surface, it seems reasonable therefore to expect alcid detection probabilities to be mid way between those of penguins and those of prions.

#### ***3.4.2 Adjusting for penguins present but not detected***

The influence of dive behaviour on detection probability was estimated individually for macaroni and gentoo penguins. However, macaroni and gentoo penguins were considered to be of similar size and appearance when on the waters surface, for these reasons corrections for distance from the observer and for sea state were estimated for both penguin species combined.

##### ***Distance***

The probability of sighting penguins decreased rapidly beyond 100 m from the observer, with the curve describing the decay being very similar to that for Antarctic fur seals (Figures 2.5, 2.6 and 2.7). The curve also showed a higher sightings probability within the 51 to 100 m distance band than within the nearest, 0 to 50 m band, a shape often indicative of ship avoidance behaviour (Buckland et al. 1993a). There was no other evidence of ship

avoidance and when penguins were sighted near the vessel, other than to avoid collision, they showed little repulsion from it.

### *Sea state*

There were six observation periods where high numbers of penguins were observed; these observations were all made all during sea state five conditions. It is likely that where large groups of animals are sighted, sea state is less likely to be of influence, as the animal group would be sighted regardless of sighting conditions. So that allowance could be made for the observation periods with fewer animals sighted, larger observations were removed from subsequent sea state analysis and were included at their unadjusted densities. With these outliers removed, sea state did reduce detection probability.

### *Allowing for dive behaviour*

Chapter Two demonstrated the importance of considering animal behaviour in the interpretation of survey results. For seals in Chapter Two, these behavioural data **were** gathered for individuals concurrently with the cruise. For penguins, behavioural data from the literature were used to incorporate an understanding of dive behaviour. This proved important, and accounted for an increase in the estimated density of 132% and 150% for macaroni and gentoo penguins respectively. This large increase in the estimated density demonstrates how important it is that studies combine behavioural data gathered from individual based studies wherever it is available. There are great number of studies applying individual or population based approaches to estimating population abundance or distribution, but is in

the integrations of these two methods that may enable greater insights to be found.

The dive model was found to be most sensitive to the total proportion of time the animal spends at the surface. Actual dive duration was less important. Macaroni and gentoo penguins both spent approximately 48% of their time at the surface. Gentoo penguins however had longer average dive duration than macaroni penguins (Williams et al. 1992; Trathan and Croxall 2004), this accounts for the larger total increase in density for gentoo penguins.

#### ***3.4.2 Penguin distribution***

Division of penguin density into sub-regions within the study box revealed very few penguins in areas beyond the 500 m isobath. Given that penguins showed strong habitat preferences, consideration of density is much more informative within these sub-regions rather than diluting the density of penguins observed on shelf by the area of the artificially constructed study box. It is important that studies estimating abundances over large areas place careful consideration to finer scale distributions within the survey area.

There was a discrepancy between the sum of density in the sub-regions compared to the whole. This occurred more with species of lower density and greater variance. This problem is a product of using the arithmetic mean density on data with many zeros, and is highly negatively skewed. This should be remembered when interpreting figures, but the overall patterns illustrated remain valuable. The problem was less apparent for prions than penguins and was not a problem at all when the same procedure was followed

for Antarctic fur seals (Chapter Four) or krill (Chapter Five), where density is higher and the distribution more normal.

Previous studies of macaroni penguin distribution suggest that overall density should decrease further away from the island (Trathan et al. 1998b), but also that density should increase around the shelf break region (Hunt et al. 1986; Hunt et al. 1992; Barlow et al. 2002; Trathan and Croxall 2004). No preference for the shelf break region was seen in this study, though whether there were insufficient observations to show this pattern or whether the pattern was not present is unclear.

Telemetry studies of macaroni penguin distribution have revealed preferences to forage out to the west of South Georgia towards Shag Rocks (53° S, 48° W) during crèche. However, during brood guard, at the time of this study, penguin use the continental shelf area and so this area must still be considered as a major foraging ground (Barlow and Croxall 2002b; Trathan Trathan and Croxall 2004; Trathan et al. in press).

### ***3.4.3 Prion observability and densities***

Prions were observed in 35% of observation periods, and the unadjusted density of prions observed was 25.44 ( $\pm$  95% CI 13.16, 37.72) birds km<sup>-2</sup>. Prions are surface feeders and so no adjustment was made for diving, nor did sea state have any significant influence on the numbers of prions observed. The only adjustment applied to the count data was made for the decrease in detectability with increasing distance from the observer. Final, adjusted, density estimates were 27.01 ( $\pm$  95% CI 13.97, 40.05), a percentage increase of 6%. Variance estimates for prions (CV = 56%) were higher than



for other avian predators (CV = 21 and 23% for macaroni and gentoo penguins respectively), this is most likely due to the large flock sizes that prions sometimes form.

The DISTANCE decay curve did not show a strong decrease in prion detection probability with increasing distance from the observer. There were more animals in the nearest distance band (0-50 m) than in any further band, but there were more animals sighted in the furthest distance band, 201-300 m, than in the central, 101-200 m band. The hazard-rate model provided a suitable fit to the data. Overall the number of prions observed was little influenced by the factors normally influencing detection probability. Prions are usually sighted within large groups and it may be that the observer, irrespective of conditions, will spot these groups. There is a potential for error in counting the number of prions within these large groups, consequently two independent estimates of the numbers of prions within the same group would help to assess the extent of this.

#### ***3.4.4 Prion distribution***

There are no previous published estimates of prion density or distribution in the South Georgia region. As such there is no base line with which to compare the results of this survey. Prions were found in all areas of the WCB, but their density was much higher over the continental shelf, within the 500 m depth isobath. Interestingly, prions showed strong and consistent preference for the shelf break region, especially along transects 3.2 and 4.1, near the 200 and 500 m isobaths. This pattern was also consistent between the two replicate surveys. Previous studies of feeding flocks of seabirds feeding

on krill around South Georgia found strong relationships between the distribution of prions, other predators and patches of krill (Harrison et al. 1991; Goss et al. 1997).

#### ***3.4.5 Comments to future surveys***

This survey was well designed for measuring the distribution of krill and Antarctic fur seals, however given the smaller area used by smaller penguins and seabirds, future surveys would benefit from concentrating on a finer scale survey on-shelf.

Interestingly, the low density of the penguins and prions observed in this study highlighted the advantage of the 300 m wide transect width over the 100 m wide strip transect suggested for Antarctic fur seals in Chapter Two. Providing one can concurrently assess the relationship between the number of animals observed and the numbers of animals present, it should not matter how many animals are actually seen. However, with a lower number of observations and a smaller survey area, the ability to accurately measure the proportion of animals missed, is reduced.

It may be that future surveys would do better with a dedicated penguin observer, and also by trying a different survey platform such as a yacht, or vessel that may have different repulsion/attraction properties.



## **CHAPTER FOUR**

### **The use of satellite telemetry and ship-based transect approaches to determining the spatial distribution and habitat preference of Antarctic fur seals at South Georgia**

#### **4.1 INTRODUCTION**

Describing the distribution of animals in space is an essential component of understanding an animal's behaviour, helping to explain its evolution and ecology. From a management perspective understanding animal distribution is essential, as by highlighting those areas most important to a species, managers can alleviate potentially harmful anthropogenic impacts. Long-term changes in the use of an environment by a population may reflect changes in population size or other aspects of its ecology. Such changes may also indicate long-term changes in its prey populations and may relate to much larger fluctuations or shifts in the ecosystem. By understanding the underlying factors driving a population's distribution it is possible to produce models to predict its distribution in un-surveyed areas, the distribution of its prey in these areas, or the potential effects of large-scale habitat changes.

Many approaches to recording, describing and modelling distribution and habitat preferences have been developed (Tasker et al. 1984; Hammond 1990; Jansen et al. 1998; Maravelias 1999; Guisan and Zimmermann 2000; Rosenstock et al. 2002; Alonzo et al. 2003a; Matthiopoulos 2003b;

Granadeiro et al. 2004). Two approaches that have been commonly used to investigate the spatial distribution of animals at sea are remote telemetry or satellite tracking (from here on termed ‘telemetry’), and visual surveys usually ship or aircraft based counts along transects (from here on called ‘transect’). These techniques can be considered respectively as individual and population approaches (Hammond 1986; Bengston 1993; Ralls et al. 1995; Udevitz et al. 1995; Cassey and McArdle 1999; Macleod et al. 2003). Both techniques have advantages and disadvantages. Telemetry has given great insight into the behaviour and ecology of individual animals (e.g. Boyd et al. (2001)), however, such studies are often limited to a small number of the overall population, often restricted to a particular life-history stage and amenability to instrumentation.

Transect surveys at-sea potentially allow information to be gathered for all components of the population using a specific area and often provide collateral information such as the proximity to other individuals (Tershy 1992), other species (Camphuysen and Webb 1999), prey (Mehlum 1999) or their environment (Hunt 1991) that would be unavailable via telemetry, though see Hooker et al. (2002). The method does not normally provide information about the status of individual animals sighted, thus knowledge of parameters such as sex, age or reproductive condition is usually absent.

At South Georgia there is a good understanding of the foraging distribution of lactating female Antarctic fur seals (*Arctocephalus gazella*) but little knowledge about how representative this is of the population overall.

Thus our ability to extrapolate from our understanding of these individual to the whole population is limited.

#### **4.1.2 This study**

Antarctic fur seals are a key component of the ecosystem around South Georgia and understanding the foraging distribution of the whole population is essential for quantifying the distribution of demand for krill (*Euphausia superba*) around the island and hence for understanding local ecosystem dynamics.

The peak in local demand for krill at South Georgia is during the breeding season (November-March) when predators have dependent offspring that remain ashore (Boyd 2002a). During this period not only is the demand for krill greatest but also the area from which it can be obtained is restricted by the need to return to land to feed offspring (Barlow et al. 2002). This Central Place Foraging (CPF) behaviour (Orians and Pearson 1979) has made satellite telemetry of lactating females relatively easy, and has resulted in a high level of understanding of the foraging behaviour of these animals during the breeding season such that data sets extend back over a decade (Boyd et al. 1991; Boyd et al. 1994; Boyd 1996; Boyd et al. 1998; Boyd 1999; Boyd et al. 2001; Boyd et al. 2002; Staniland and Boyd 2003). However, for the remainder of the population, such as juveniles, non-breeding females and males, where tag recovery is less predictable, financial and logistical constraints mean that they are less well understood, whilst the need to understand them is essential.

The aims of this chapter are thus two fold (1) to compare the foraging distribution of Antarctic fur seals from transects with that of lactating female fur seals, derived by telemetry, i.e. to answer the question: Can the distribution of female lactating Antarctic fur seals foraging from Bird Island be used as a proxy for the whole population? And; (2) to describe the at-sea distribution of Antarctic fur seals to the northwest of South Georgia in terms of relationship to their prey and to the physical characteristics of their ecosystem.

At-sea surveys were conducted in the area known from previous studies (Boyd et al. 2002), to be used by telemetry-tracked lactating females in order to compare the simultaneous distributions of lactating females and all seals in the area. All transects were repeated with a minimum of five days between replicates. This is the first study to combine concurrent individual (telemetry) and population (transect) based approaches to describe the at-sea distribution of otterid seals. The relationship between Antarctic fur seals and krill is also investigated. By understanding the nature of this relationship we will not only gain an understanding of what influences seal distribution, but also knowledge of seal distribution to further our understanding of krill distribution.

Similarity in distribution patterns may be combined between different data sets at different scales, such that the similarity between the following can be compared:

- The qualitative distribution from telemetry and transect methods.
- The distribution of seals from transect methods along replicate transects.
- The distribution of seals from transects and the distribution of the telemetry data along the same lines.
- The distribution of krill along replicate transects.
- The distribution of seals and krill from along the same transects.
- The distributions predicted by GAM models, built on the relationships between transect and telemetry-derived distributions and the physical environment.

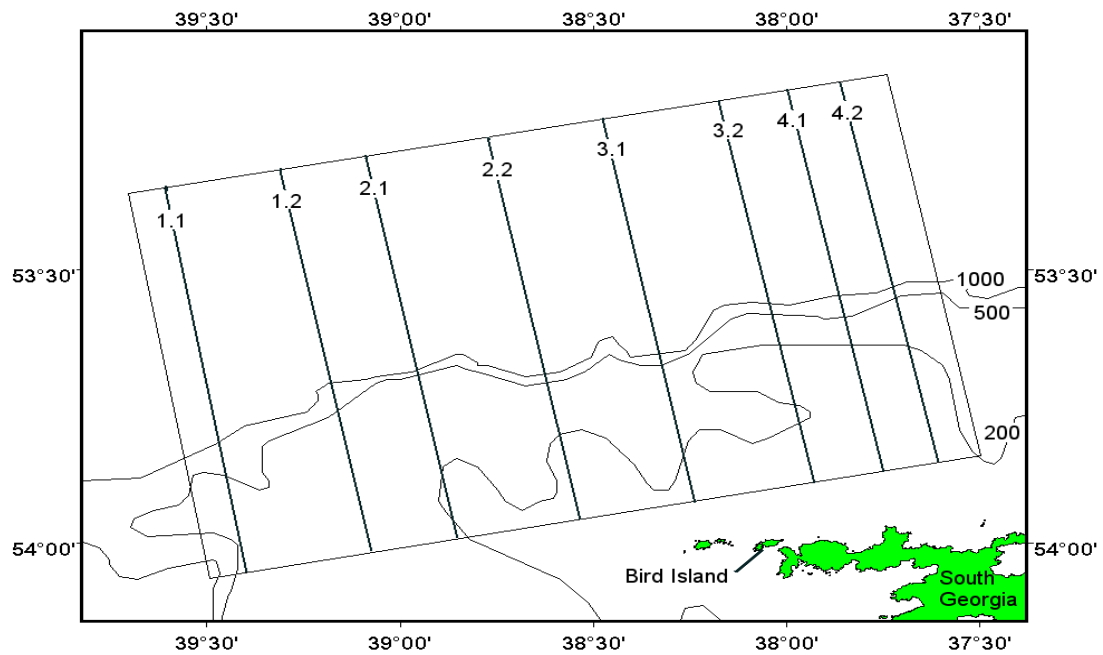
## **4.2 METHODS**

### ***4.2.1 Data collection***

#### ***Survey design***

This study was conducted in the British Antarctic Survey long-term study area, termed the Western Core Box (WCB) (Figure 4.1) to the northwest of South Georgia (Atkinson et al. 2001; Trathan et al. 2003) during January-February 2002. This is in an area where lactating female fur seals from Bird Island are known to forage (Boyd 1999; Staniland et al. 2004).





**Figure 4.1.** Map showing the layout of transects and the study area. Also shown are the 200, 500 and 1000 m depth isobaths.

### *The distribution of fur seals along transects*

The survey was designed to provide a quantitative estimate of krill density and transects were aligned perpendicular to the continental shelf break, the dominant topographical feature of the region (Trathan et al. 2003). On each day of the survey two 80 km transects were surveyed with the ship maintaining a speed of ~10 kts. All transects were surveyed twice with a gap of five days between replicates. Observations were made over an area of sea 300 m forward and to one side of the ship. Sightings were recorded in one of four distance bands (0-50 m, 51-100 m, 101-200 m and 201-300 m) perpendicular to the transect line. Observations were made continuously and were summed into 5-minute periods, following the methodologies of Tasker et al, (1993) as adapted by Van Franeker (1994), and analogous to methods used in previous studies in the region (Hunt et al. 1986; BIOMASS 1992;

Hunt et al. 1992; Van Franeker 1994; Whitehouse and Veit 1994; Veit 1995; Trathan et al. 1998b).

Adjustments were made for factors that may reduce the probability of detecting an animal including, distance from the observer, sea state, and dive behaviour. This provided a density estimate of seals  $\text{km}^{-2}$  with a minimum spatial resolution of ~1.6 km along the transect. The survey methods used to provide density estimates are described in more detail in Chapter Two.

### ***Measuring the distribution of fur seals at sea using telemetry***

A total of 59 female Antarctic fur seals were tracked from Bird Island between 03/01/02 and 04/03/02. Each animal was tagged over a single foraging trip lasting between 3 and 16 days.

Platform Transmitter Terminals (PTT, ST10, cast A-400, 13 x 4 x 2 cm, 200 g, Telonics Inc., 932 E. Impala Avenue, Mesa, AZ 85204, U.S.A.) were attached with epoxy glue to the fur along the dorsal midline between the scapulae (Boyd et al. 1998). PTT signals were received by the ARGOS satellite system (CLS Argos, 18 Ave Edouard Belin, 31005 Toulouse, France). Upon the seal's return to the study colony, the telemetry equipment was removed.

### ***Accuracy of geographical location from PTTs***

The ARGOS system allocates a Location Quality Index (LQI) to each location fix according to the level of confidence associated with the location provided. This confidence is based on the number of uplinks received by different satellites associated with each fix. At least four successive uplinks during a satellite pass are required for Location classes 0 ( $\pm >1000$  m), 1 ( $\pm$

350 – 1000 m), 2 ( $\pm 150 - 350$  m) or 3 ( $\pm \leq 150$  m), however, some fixes with less uplinks may still be useful (classes A, B or Z) (McConnell et al. 1992; Boyd et al. 1998; Vincent et al. 2002; Phillips et al. 2004). Boyd et al. (1998) quantified the degree of error associated with each of these classes by examining the locations received from two PTTs placed at a known location. The average location, provided by ARGOS for the transmitter placed at the known location, was within 1-2 km for the location classes 1, 2 and 3, with the maximum distance from the site being 6 km. On average, location class 0 gave a position of 3.8 km from the correct location; with a maximum distance of 8.6 km. Location classes A and B had maximum errors of 130 km.

Locations with LQI values 0, A, B and Z may still carry valid location data. For this reason the data was filtered by testing for the velocity required to travel between uplinks using the iterative forward-backward averaging filter described by McConnell et al. (1992). A velocity ( $V_i$ ) was associated with the  $i^{th}$  location such that:

$$V_i = \sqrt{\frac{1}{4} \sum_{j=-2, j \neq 0}^{j=2} (v_{i,j+i})^2} \quad \text{Equation 4.1}$$

Where  $v_{i,j}$  is the velocity between successive locations  $i$  and  $j$ .

Locations with  $V_i$  greater than the estimated maximum velocity of a seal ( $2.5 \text{ m s}^{-1}$ ) were rejected, based on swimming speeds described by Boyd et al. (1998) and as used by Boyd et al. (2002). The filtering process resulted in the rejection of 17.8% of all uplinks, with rejection in different LQ classes as: Class B = 75%, Class A = 24%, Class 0 = 18%, Class 1 = 8%, Class 2 =

4%, Class 3 = 5%. Leaving 4994 uplinks over 59 individual foraging trips, this is summarized in Table 4.1.

**Table 4.1. The number of uplinks within each Location Quality Class, and the number filtered out from each class.**

Location Quality	<i>n</i> start	<i>n</i> rejected
3	81	4
2	281	12
1	1263	103
0	1440	263
A	1217	299
B	1678	1275

### ***Data smoothing***

One approach to the initial visual comparison of two distributions is to generate a continuous smoothed surface. Each observation point carries information about neighbouring locations and smoothing aims to redistribute the information contained in a way that takes account of positive autocorrelation and reduces random variability (Seaman and Powell 1996; Matthiopoulos 2003a).

Kernel smoothing works by placing a probability density function (the kernel) centred over the target point and covering a neighbourhood around that point. The shape of the kernel may take a number of forms such as a square, triangle, or the most commonly applied, and also the one used in this study, gaussian. The kernel surface was only generated for that part of the 95% home range polygon of the telemetry data, i.e. the area where the animals spent 95% of their time, that fell within the area of the study box.

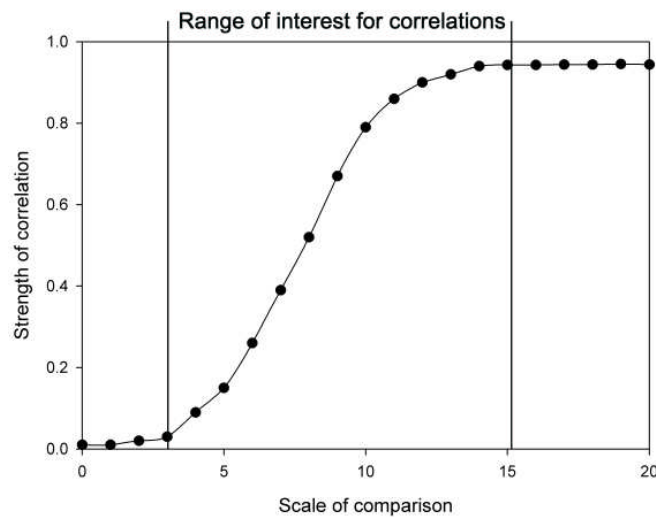
The choice of the smoothing parameter ( $h$  – the spread of the kernel around the data point) determines the level of smoothing. In choosing  $h$  it is

important to reconcile the potential effects of choosing a value that is too high resulting in the loss of information about the data distribution and an  $h$  that is too small and the objective of the procedure is not accomplished. Hence the aim is to choose a value of  $h$  that provides an intermediate level of smoothing (Gitzen and Millspaugh 2003; Matthiopoulos 2003a). The appropriate value of  $h$  was determined by least-squares-cross validation (LSCV) (Silverman 1986; Gitzen and Millspaugh 2003). LSCV is a common method that allows  $h$  to be chosen so as to minimise the difference between the predicted surface using all the data and one fitted excluding the data point (Hemson et al. 2005). LSCV was estimated using available routines in the software package R (Wood 2001). A kernel with  $h=0.02$  was chosen.

### ***Scales of correlation***

In a similar way to choosing the correct smoothing factor for kernel analysis, choosing the correct scale for comparing distributions is essential. Previous studies have shown relationships between predators and prey differ with the spatial scale at which they are measured. In particular these relationships may show no correlations at smaller scales and significant positive relationships at larger scales. Nevertheless, at the finest scale a relationship between predator and prey must exist as a predator has to eat (though this may depend on fine scale temporal as well as spatial resolution). The scale-dependency of these processes and the effect on measuring correlation means that positive relationships may only become apparent at larger scales, yet at these larger scales we also know that relationships must exist, a plot showing that both krill and fur seals are found within 100 km of

South Georgia is largely uninformative (Schneider and Duffy 1985; Schneider and Piatt 1986; Hunt and Schneider 1987; Rose and Leggett 1990; Hunt et al. 1992; Ritchie 1998; Fauchald 1999; Mehlum 1999; Reid 2001b; Davoren et al. 2002). With the serendipitous relationships that may potentially be expected in this kind of study, only making the comparison at one scale could lead to false interpretations of an unstable relationship that may be better revealed by investigation over a range of scales. Figure 4.2 illustrates how one may expect the strength of correlation to increase with the scale of comparison and highlights the range of highest ecological interest.



**Figure 4.2.** Idealized illustration of how we may expect the strength of correlation to increase with the increasing scale of comparison. Insufficient relationships may be found at smaller scales and beyond the asymptote the correlation is less meaningful and may be at a scale that no longer allows insight to the underlying processes.

### ***Krill density along transects***

Within each transect krill density was estimated using a Simrad EK500 echosounder operating hull-mounted 38, 120 and 200 kHz transducers. Synchronous pulses from all transducers were transmitted every 2.5 seconds. 120 kHz Sv values identified as originating from krill targets

were converted to average krill densities. For further details of target identification, target strength determination and calibration procedures see Brierley & Watkins (1995).

The minimum krill resolution available along transects at 2.5 second intervals was much smaller than that available for fur seals, and so krill density was averaged into bins along the transect at a scale to match those of fur seal densities. Correlations were assessed based on data from the whole acoustic interrogation depth (250 m) and to a depth representing the depth at which krill remains available to Antarctic fur seals (50 m).

### ***Bathymetry***

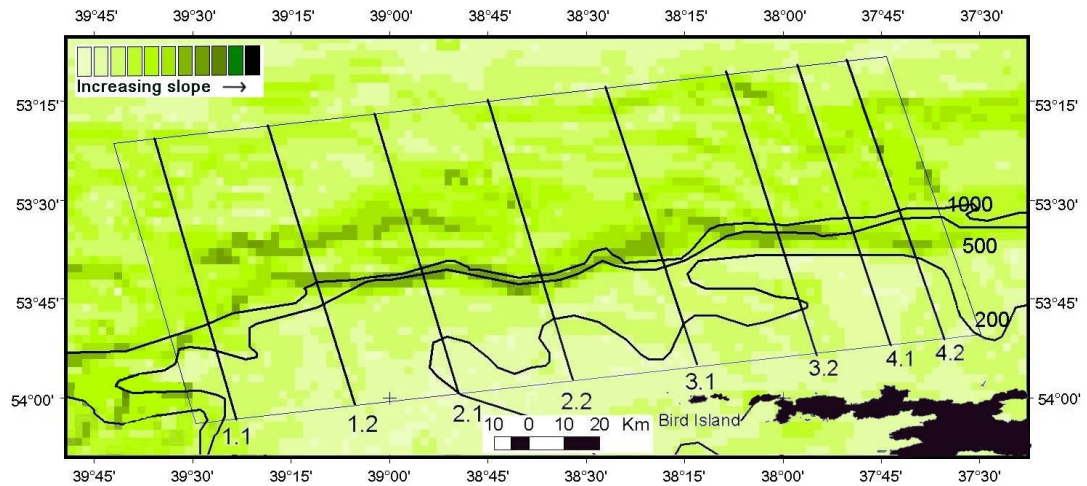
Depth was calculated from a raster layer in ArcInfo 8.0 GIS software (Environmental Systems Research Institute Inc., 1992-1999) with a spatial resolution of 0.001' x 0.001' (~1.716 km<sup>2</sup>). This layer was created by amalgamating all available depth records for the South Georgia region to create the highest resolution bathymetric map for the area. The bathymetric slope for each cell was calculated using the Spatial Analyst function of ArcInfo as the steepest slope between each cell and the surrounding eight cells.

$$\text{Percentage slope} = \frac{|rise|}{run} 100 \quad \text{Equation 4.2}$$

Where *rise* is the difference in depth (m) between two cells and *run* is the distance between their centre points (m).

For subsequent analysis both the slope and depth layers were converted from raster to grid layers (a raster describes an area defined by its

(often irregular) contours, and a grid has a series of regular cells). Slope and depth values were then derived from these grid layers for any point of interest by using the Grid Analyst extension to ArcView 3.2 (Environmental Systems Research Institute Inc., 1992-1999).



**Figure 4.3.** Grid of bathymetric slope within the study region. Also shown are the 200, 500 and 1000 m depth isobaths.

### *Distance to land*

Distance to land was calculated as the great circle distance to the study colony based on Bird Island for the satellite data and to the nearest point of South Georgia coast line for the transect derived data set. This was calculated using the Haversine formula (Gellert et al. 1989), in the form:

$$\text{Distance} = 120.\text{deg} \cdot a \sin \sqrt{\sin^2 \left( \frac{x_2 - x_1}{2} \right) + \left( \cos(x_2) \cdot \cos(x_1) \cdot \sin^2 \left( \frac{x_2 - x_1}{2} \right) \right)}$$

Equation 4.3

Where  $x_1$  and  $x_2$  are the locations in decimal degrees of the points between which distance is measured. This was calculated firstly for latitude ( $x$ ) and secondly for longitude ( $y$ ), with the total distance ( $z$ ) estimated as:



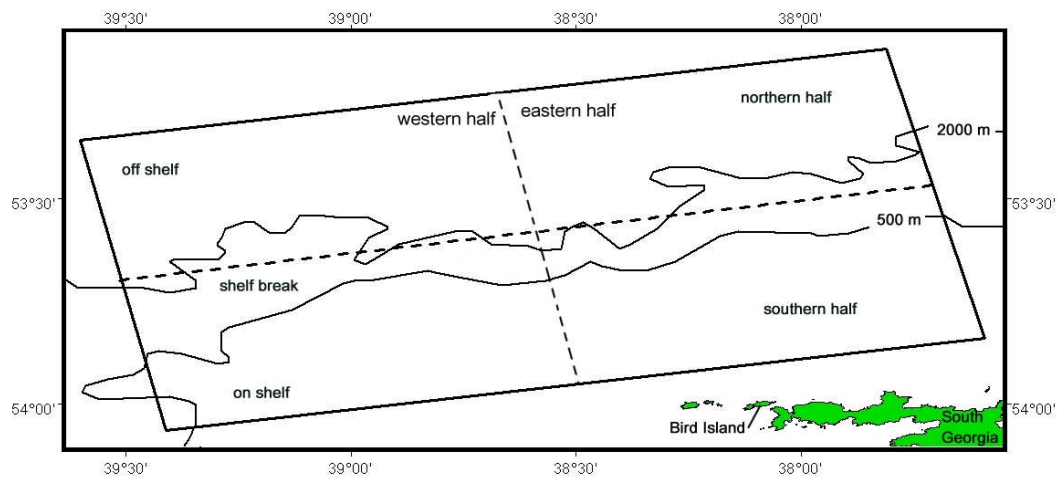
$$z = \sqrt{x^2 + y^2}$$

Equation 4.4

### 4.2.2 Data Analysis

#### *General patterns in distribution*

Differences in seal density were examined: (1) between the northern and southern sectors of the study box (defined by a line running between 53°.72 S, 39°.59 W and 53°.46 S, –37°.63 W), (2) between the eastern and western sectors of the study box, defined as east and west of 38°.6 W longitude (the mid point of the study box) and (3) between regions defined by depth as follows: on-shelf (shallower than 500 m), shelf break (500 – 2000 m deep) and off-shelf region (deeper than 2000 m). Density data were non-normally distributed and so the differences in density between regions were investigated by comparing the medians using a Mann Whitney U test.



**Figure 4.4.** Map showing Western Core Box study area and spatial divisions based on depth (with cut points at 500 m and 2000 m), eastern and western and northern and southern sectors of the area.

***Differences between the satellite and line transect derived distributions***

The differences between the distributions of Antarctic fur seals derived by telemetry and transect methods were investigated by three different methods; (1) by qualitatively comparing two smoothed overall usage surfaces, (2) by using ‘virtual transects’ where the distribution of telemetry tracked seals falling along transect lines were compared with the distribution of seals along the transect line from the transect data. These were accompanied at different spatial scales and (3) by modelling the distribution of seals using General Additive Models (GAM) using the telemetry and the transect data, and comparing the distributions of seals for the whole WCB predicted by the models.

***4.2.3 Relationships between variables along transect lines***

Various comparisons were made along transect lines, these comprised:

- Seal density between replicate transects.
- Seal density between transects and virtual transects through the telemetry derived distribution (4.2.4)
- Krill density between replicate transects (4.2.5.a)
- Between krill and seal density along transects (4.2.5.b)

Each of these comparisons had their own individual differences but the general procedure was applied as follows:

Correlations between variables were all investigated at increasing spatial scales. Observations were grouped into 0.02° (~2.22 km) bin lengths along each transect. This scale provided the finest resolution possible whilst ensuring that at least one observation node from both variables were included.

These values were then compared using Pearson's product moment correlation co-efficient, on ranked data, at increasing spatial scales, such that comparisons were made between bin lengths of 2.22 to 26.68 km (Veit et al. 1993). Data were grouped into increasing spatial scales using a moving average. For example, the minimum bin length was 2.2 km, this was increased to 4.4 km so that the first 4.4 km bin =  $\bar{d}_{1,2}$  and the next cell along the transect =  $\bar{d}_{2,3}$  etc. A moving average was chosen as a smother in preference to a kernel based smoother due to its simplicity and ability to keep scales in km, both were tried, with little difference between the two.

#### ***Estimating correlation significance***

Due to the autocorrelation in the data, testing the significance of the correlations using formal probability scales was inappropriate. Therefore randomisation tests were used to evaluate statistical significance for each scale and transect compared. Values of  $r$  and their significance were obtained by randomly allocating density values from one of the transects to a different location along the same transect, and calculating the correlation with the other transect. This randomisation and correlation procedure was repeated 1000 times. The transects were considered to be significantly correlated where the observed value of  $r$  exceeded 95% of these values.

#### ***4.2.4 Virtual line transects***

Comparisons were also made between the telemetry and transect distributions within the range of overlap (within the 95% kernel home range polygon of telemetry distribution). To generate the density surface for the

telemetry distribution, we used the number of uplinks within each cell. These distributions were then compared using the procedures outlined in section 4.2.3.

#### ***4.2.5 Factors underlying the seal distribution***

We know that the distribution of krill must influence the distribution of Antarctic fur seals, and it may be changes in krill distribution result in changes in seal distribution. Therefore, prior to seal-krill comparisons, the distribution of krill between the two replicate surveys was compared at similar spatial scales as those used for seals.

One reason for understanding the distribution of animals is to develop models that allow the prediction of animal distribution in un-surveyed areas or at un-surveyed times. To base such models of the distribution of prey requires knowledge of prey distribution therefore it makes more sense to derive models of an animals distribution based on abiotic factors that either remain constant over time such as the physical characteristics of the environment or based on variables that can be determined remotely.

We dealt with these two relationships separately, firstly investigating the relationship between fur seals and krill and secondly, between fur seals and the physical characteristics of the environment in a habitat preference model.

##### ***4.2.5.a. Relationships in krill distribution between replicate surveys***

The relationship in krill distribution between replicate surveys was assessed using the same rank and randomisation methods as described in section 4.2.3 at increasing spatial scales between 2.22 to 26.68 km.

***4.2.5.b. Relationships between Antarctic fur seals and krill***

The relationship between Antarctic fur seals and krill was also assessed using the same rank and randomisation methods as described in section 4.2.3 at increasing spatial scales between 2.22 to 26.68 km. Correlations were carried out for krill to both 50 and 250 m depth horizons.

***4.2.5.c. Habitat preference models******Fitting of the model***

The relationships between seal distribution (derived from both survey methods) and physical data were explored using Generalised Additive Models (GAM's). The GAM is a regression method that relaxes the restrictions of normality and linearity inherent in linear regression. GAM's use spline functions (Ihaka and Gentleman 1996; Clarke et al. 2003; Wood 2003); splines allow the function to be fitted by interpolation and allow for a more flexible and closer fit to the response variable than would be gained using simple linear predictors. GAM's were fitted in the package *mgcv* (multiple generalised cross-validation) for the program R (Wood 2001). This inherent flexibility in the model could result in over fitting of the model. To avoid this, the approach uses penalised regression splines, where each spline carries a penalty for excessive flexibility (Wood 2000; Wood 2003). Overall bounds of the model are determined by knots. Knots are controlling values, which essentially set the boundaries of the model relationship. They are approximately one higher than the estimated degrees of freedom, *df*, for each model term (Wood 2001).

The amount of flexibility given to a model term is determined in a maximum likelihood (GCV) working in the same way as that described for LSCV in section 4.2.1 such that the error is reduced to the minimum GCV score for the whole model, rather than each component.

The model framework was of the form:

$$n_x = \sum_k f_k(z_{xk}) \quad \text{Equation 4.5}$$

Where:

$n_x$  = the density of animals in cell  $x$ ; and  $z_{xk}$  = represents the value of the  $k^{th}$  explanatory variable in the  $x^{th}$  cell, which is a smooth function,  $f_k$  of the explanatory variable.

The default smoothing value for one-dimensional splines was used in the package mgcv, 10 knots in each spline were allowed corresponding to 9  $df$  (Wood 2001; Wood 2003). The response variable was drawn from a Poisson distribution, as used by previous GAM models based on clustered populations (Maravelias 1999; Maravelias 2001; Granadeiro et al. 2004).

Whilst the optimal amount of smoothing is automatically determined by GCV, the decision whether to include or drop a model term is not. Potential explanatory variables considered for inclusion in the model were *depth*, *slope*, *aspect*, *distance from land*, *latitude* and *longitude*. The following summarises the applied model specification procedure, using the structure proposed by Wood (2001):

Saturated models were fitted. E.g:

$$(y \sim s(\text{depth}) + s(\text{distance}) + s(\text{slope}) + s(\text{aspect}) + s(\text{latitude}) + s(\text{longitude}))$$

Equation 4.6

Where  $s$  = the smoothing factor, in this case the default value.

- If any model term approached the maximum flexibility allowed (9  $df$ ), then the number of knots allowed for that term was increased to 20, and the models refitted.
- Model fit was assessed using the `summary.gam` and `plot.gam` functions in `mgcv`, which showed coefficients, GCV score, explanatory power (deviance explained) and fit (residual plots).
- The model with the lowest GCV score was chosen.
- For each model term where explanatory power was very weak, or the 95% confidence interval crossed zero, the term was dropped and the GCV score re-assessed.
- The telemetry derived response variable was calculated from the kernel-smoothed surface generated as described in section 4.2.1. For this, the probability density value was taken from the same node of each grid cell used in calculating the explanatory variable. The transect derived response variable was taken from the density value (seals  $\text{km}^{-2}$ ) associated with each five-minute observation period.

#### **4.2.6 Predicting distribution**

Each GAM was then used to produce a predicted seal density for each  $0.01^\circ$  cell in the WCB using the “`predict.gam`” function of the `mgcv` package

(Wood 2001). The predicted distributions were then compared using the randomisation procedure described in 4.2.3, in this case all cells in one grid were assigned values at random. This relationship, like others in this study, was investigated at increasing spatial scales from  $0.01^\circ$  to a scale found to be greater than the asymptote in other comparisons,  $0.6^\circ$ .

## **4.3 RESULTS**

### ***4.3.1 General patterns in distribution***

#### ***Patterns in density***

The transect survey found a greater median density of seals in the southern half of the WCB than the northern half (Mann-Whitney U:  $n = 794$ ,  $w = 47536$ ,  $p = 0.011$ ) and between the density of animal's on-shelf (shallower than 500 m), and in the off-shelf region (deeper than 2000 m) (Mann-Whitney U:  $n = 358$ ,  $w = 30295$ ,  $p = 0.023$ ). There was no significant difference between the median density of seals in western and eastern sides of the WCB (Mann-Whitney U:  $n = 794$ ,  $w = 40171.5$ ,  $p = 0.172$ ) nor between the shelf break region (500 – 2000 m) and either the shallow region (Mann-Whitney U:  $n = 221$ ,  $w = 17771$ ,  $p = 0.42$ ) nor deep region (Mann-Whitney U:  $n = 265$ ,  $w = 9098$ ,  $p = 0.27$ ).



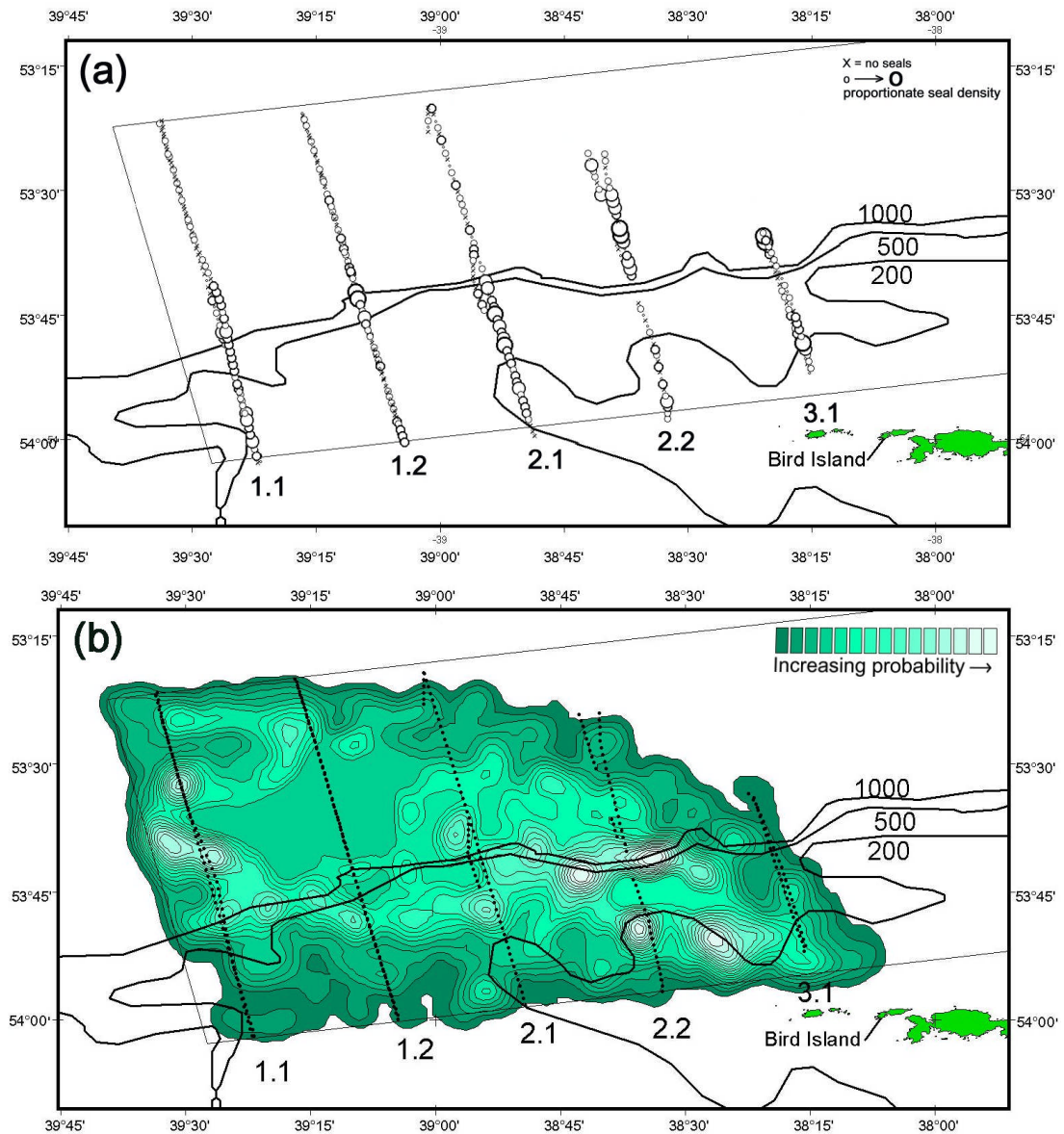
**Table 4.2. Median density and quartiles of Antarctic fur seals in different sectors of the study area.**

Area	Median density	Q1, Q3
Whole box	20.50	0, 51.55
On shelf	21.39	0, 61.31
Shelf break	19.77	0, 31.81
Off shelf	16.29	0, 39.83
Southern section	21.32	0, 59.34
Northern section	16.29	0, 33.40
Eastern section	20.33	0, 53.28
Western section	20.57	0, 46.72

***Qualitative patterns in distribution***

Lactating Antarctic fur seals foraging from Bird Island concentrated their time at sea in a polygon extending to a maximum distance of 220 km to the northwest of the colony, with a mean bearing 280° (Figure 4.5). Within that polygon, distribution was not uniform with some quite distinct regions being used more than others.

Though similarities were found between transect and telemetry derived distribution surfaces, these were more in general pattern than distinct areas. Although density was highest nearest the island, high concentrations were also seen along the shelf break region and in other distinct but smaller regions both on and off the continental shelf. Unlike the distribution from telemetry uplinks, the transect data revealed no preference for the region to the northwest of South Georgia, and overall density was highest at the eastern end of the study box, directly to the north of the island.

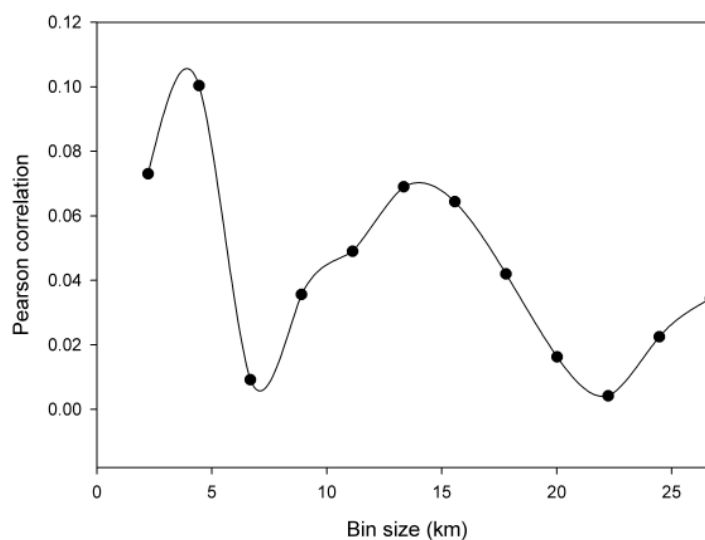


**Figure 4.5. (a) The distribution of seals from line transect, within the area overlapping the telemetry data, showing both surveys, x indicates an observation period with no seals observed and O indicate seals observed where increasing circle size is proportionate to increasing seal density and (b) Kernel smoothed surface of the density of telemetry uplinks from animals foraging from Bird Island within the overlap area. Black dots indicate line transect survey effort.**

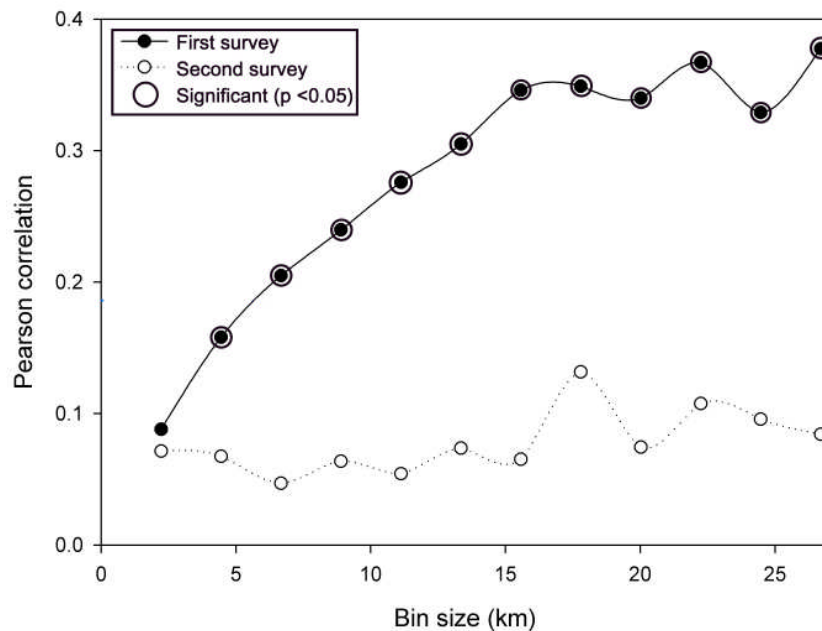
### ***4.3.2 Virtual line transects and scales of correlation***

#### ***Correlation between the first and second surveys***

The nature of the relationships between replicate transects at different spatial scales is illustrated in Figure 4.6. Overall there was no significant relationship between the distributions of seals along transects during the first and second surveys.



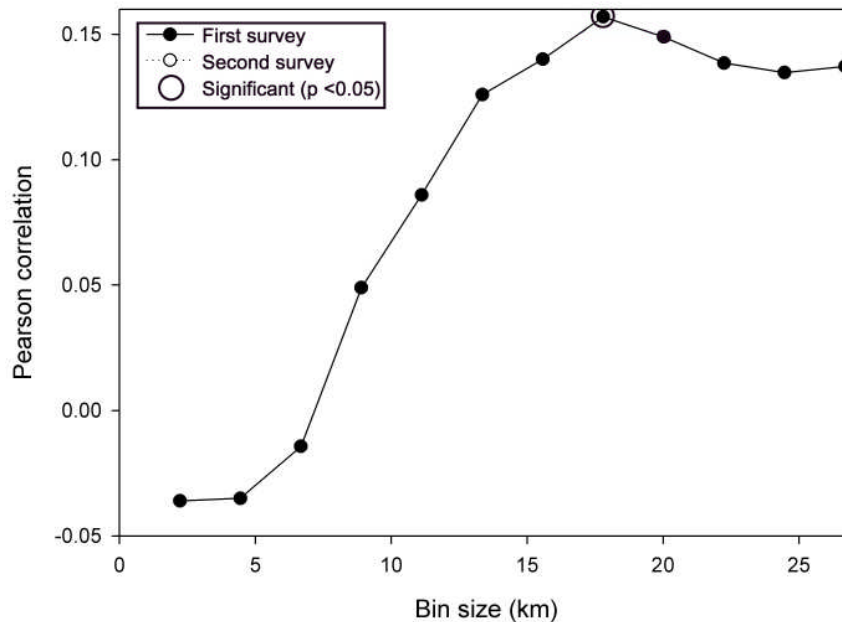
**Figure 4.6. Pearson correlations between seal abundance from the first and second surveys at bin sizes of 2.22-26.68 km.**

*Correlation between transect and telemetry*

**Figure 4.7.** Pearson correlations between seal abundance from telemetry and transect from the first and second surveys at bin sizes of 2.22-26.68 km. Significant correlations are indicated with a circle around the point.

The results of correlations between telemetry and line transects were again inconsistent. Significant relationships were found during the first survey, but not during the second. During the first survey the relationship strength did increase with increasing spatial scale, and appeared to reach an asymptote at a bin size of approximately 16 km, relationships were significant at scales beyond 6.6 km. No significant relationships were found during the second survey, and there was no evidence of a relationship even when the scale of comparison was increased to a bin size of 35.58 km.

### 4.3.3 The relationship between replicate krill surveys



**Figure 4.8.** Pearson correlations between krill abundance from the first and second surveys at bin sizes of 2.22-26.68 km where krill density is measured within the top 250 m. Significant correlations are indicated with a circle around the point, see text for further details.

A weak positive relationship was found for krill distribution between the replicate surveys. The relationship grew in strength to a peak at a scale of 17.8 km, at which point it was significant at the 95% level. Overall however, the relationship was weak and inconclusive.

#### 4.3.4 The relationship between Antarctic fur seals and krill

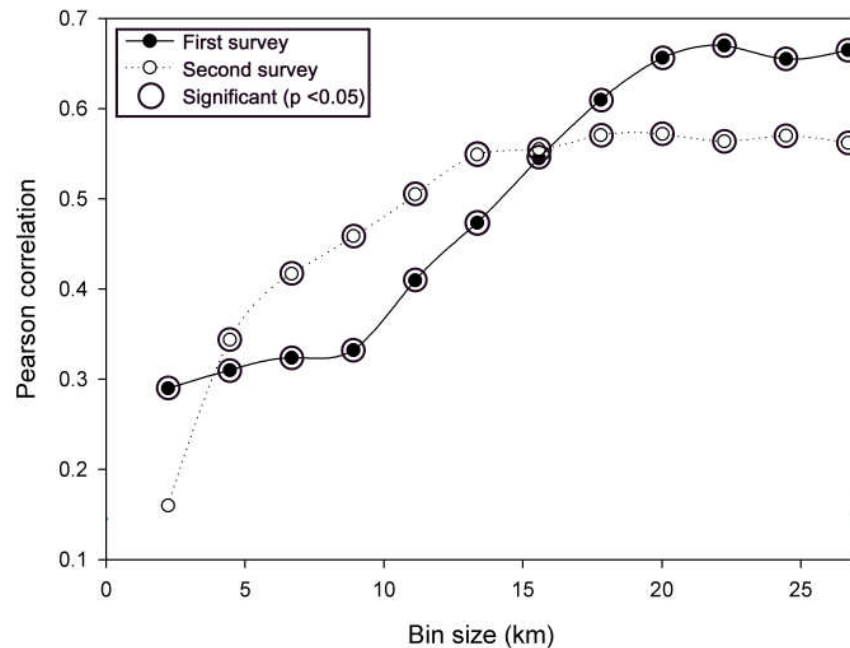


Figure 4.9. Pearson correlations between seal abundance and krill from the first and second surveys at bin sizes of 2.22-26.68 km where krill density was measured within the top 250 m. Significant correlations are indicated with a circle around the point, see text for further details.

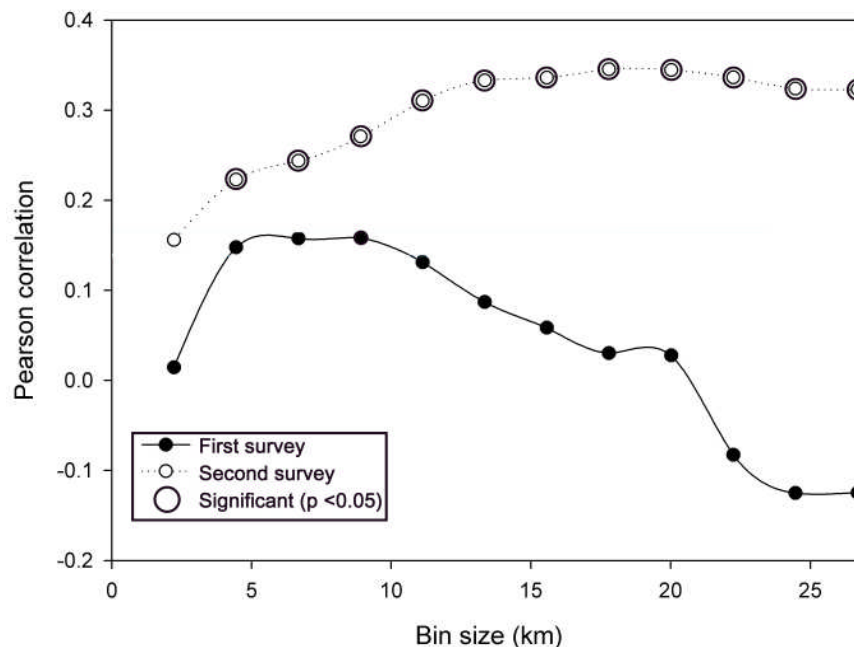


Figure 4.10. Pearson correlations between seal abundance and krill from the first and second surveys at bin sizes of 2.22-26.68 km where krill density was measured within the top 50 m. Significant correlations are indicated with a circle around the point, see text for further details.

Where krill density was considered to 250 m there was a strong significant relationship with seal density, this relationship was significant ( $p = >0.001$ ) at all scales greater than 2.2 km bin size. When krill density was considered to the 50 m depth horizon, though significant at lower spatial scales, during the first survey the strength of the relationship was reduced at scales beyond 6.6 km. For both first and second surveys the relationship between krill and seals was weaker with krill densities to a depth of 50 m than to 250 m.

#### ***4.3.5 Habitat preference model***

The selected model based on the seal distribution by transect methods was:

$$\hat{n}_s = s(\text{dist}, 7.20) + s(\text{slope}, 7.43) + s(\text{latitude}, 1.84) \quad \text{Equation 4.7}$$

Whilst the selected model based on the seal distribution by telemetry methods was:

$$\hat{n}_s = s(\text{dist}, 7.17) + s(\text{depth}, 7.95) + s(\text{latitude}, 6.47) \quad \text{Equation 4.8}$$

Where  $s$  = the smoothing factor associated with that component of the model.

The transect-based model had a high GCV score of 1783.4, with  $n = 641$ . The explanatory power of the model was only moderate and explained 12% of the deviance. The telemetry-based model was more powerful, explaining 41% of the deviance, and had a GCV score of 159. The smooth functions are shown in Figure 4.11. For both models distance from land and a

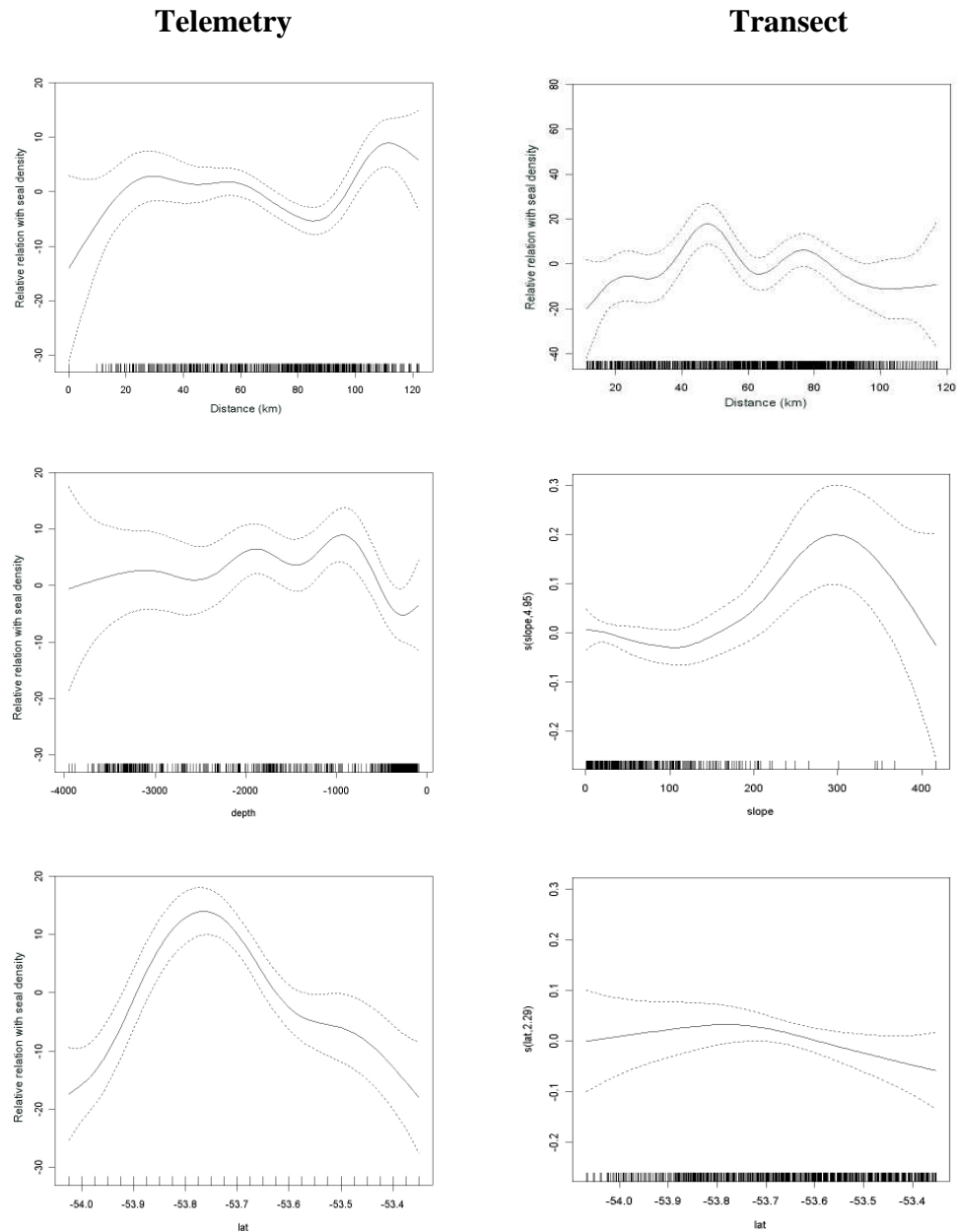
parameter representing bathymetry were the strongest explanatory variables.

The parameters aspect and longitude were disregarded from the model.

Figure 4.11 shows the fit of the model to the included parameters. Though they don't quite match, both telemetry and transect derived distributions were high at around 40 km from the island, the telemetry derived distribution additionally showed a peak around 110 km.

The relationship shown between telemetry derived distribution and depth was consistent with the known peaks around the shelf break region, with density highest between the 500 m and 1500 m contours. For the telemetry-derived distribution, the relationship was similar with the highest densities occurring with the steeper bathymetry, at these higher gradients however there were few data points. Though stronger for the telemetry derived distribution, the relationship with latitude was similar for both distributions, with the highest density occurring at around  $-53.77$  degrees.

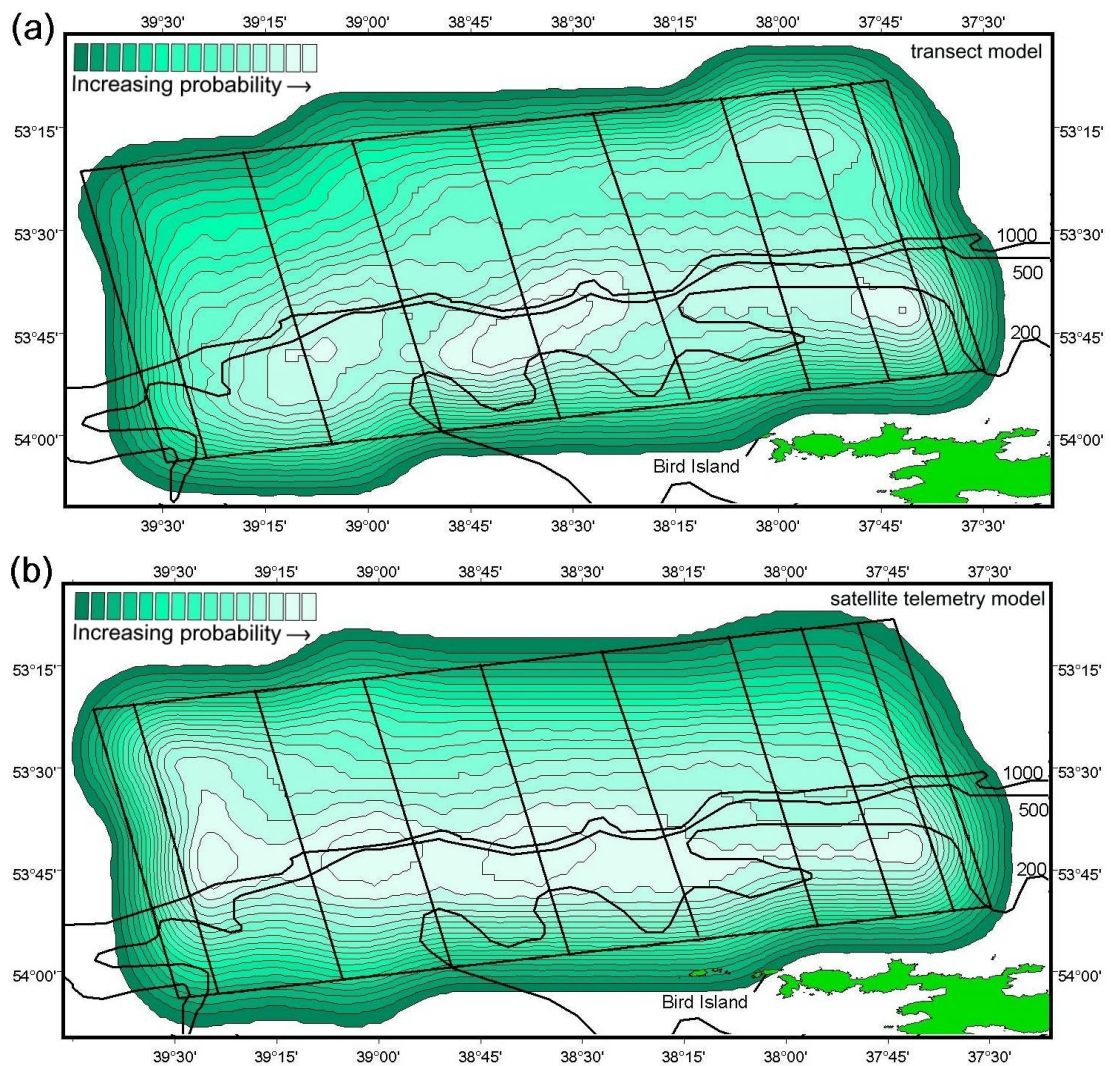




**Figure 4.11.** Smoothed components (solid line) of explanatory variables used in the fitted GAM and the response variable, relative density of Antarctic fur seals. Each  $x$ -axis contains a rugplot where small ticks indicate observations. Areas of high seal density are indicated by values greater than zero on the  $y$ -axis. Dashed lines indicate  $\pm 2$  standard errors, approximately 90% Confidence intervals.

#### 4.3.6 Predicted seal distribution across the study area

There was a strong significant positive relationship between the distributions predicted from each model ( $r = 0.377$ ,  $p = <0.001$ ) when compared at the finest scale, this relationship only grew in strength with comparisons at greater scales.



**Figure 4.12.** Kernel smoothed surface of predicted Antarctic fur seal densities from GAM models. Models are based on (a) transect and (b) telemetry derived distributions. Lighter areas indicate areas of higher density. Also shown are the 200, 500 and 1000 m depth isobaths.

## **4.4 DISCUSSION**

The aims of this study were to investigate the relationship between Antarctic fur seals and their environment and to investigate the similarity in seal distribution derived by telemetry (where distribution is described from individual, central place foraging lactating females) and by transect (where the distribution is described from the distribution of all the animals using an area).

Looking for fine scale relationships in the distributions derived from telemetry and transect was problematic. Occasional strong relationships were found, but these were inconsistent. By stepping back and looking at our understanding of the explanatory variables relating to seal distribution from the two methods, we found their distributions to be the same, and that models, based on their driving factors, predicted significantly similar distributions. Therefore it seems reasonable to conclude that our knowledge of distribution derived by telemetry can act as a proxy for the whole population. Strong relationships were also found between the distributions of fur seals and krill.

### ***4.4.1 Overall Patterns in distribution***

Based on the behaviour of satellite tagged lactating females, Staniland & Boyd (2003) found dive effort to be concentrated in three spatial clusters, indicative of seals foraging over the continental shelf, in the shelf break region and in oceanic waters. During our survey high densities of seals were found in all regions. There was a significant difference in the median number of seals between regions, with higher densities found on-shelf or in the

southern half of the box. Interestingly, we also found greater variance further away from the island. There were a lot of seals beyond the shelf, but here concentrations appear to be in localised peaks rather than in the more uniform distribution as found on-shelf. Hunt et al. (1992) found similar patterns, finding a general decay in density away from the island, but with distinct peaks off-shelf.

One difference between the telemetry and transect derived distributions was the preference shown by telemetry, of lactating females foraging from Bird Island to forage within a narrow ‘tongue’ to the northwest of the island. This pattern has been found to be consentant inter-annually (Boyd et al. 2002). The distribution of seals from the transects indicated no greater density of seals in the western half of the study box than in the east, suggesting that the overall population showed no such preference for the region to the northwest of the island. Boyd et al. (2002) examined the distribution of lactating female seals foraging from Stromness Bay (54.2° S, 36.6° W), a bay further to the east along the north coast of South Georgia. Here seals foraged mainly to the northeast, suggesting that seals forage approximately perpendicular to the coastline, heading directly towards the nearest shelf break region. However the area of shelf break closest to Bird Island is directly to the north, not to the northwest where satellite tagged lactating females were found to forage.

Seals foraging from Bird Island, are on the northwest tip of South Georgia and it may be that by heading more to the west they reduce the competition by foraging beyond the range of other animals foraging from

other locations on the South Georgia coast to the east. It could also be that the area to the northwest of South Georgia provides food of a higher quality/density, or that food is more predictably found in this region (Staniland et al. 2004).

Recognizing the difference between these two reasons for off-shelf foraging, i.e. between increased competition closer to the colony and increased prey predictability further from the colony is important if we are to understand the potential for competition between krill predators and fisheries. If seals have had to look further away than the nearest foraging areas due to increased competition, then increasing krill fisheries in this region may be problematic.

Reid et al. (2005) used transect surveys within the Scotia Sea area to identify the nature and scale of potential overlap between predators and fisheries. Their study found that abundances of krill predators, including Antarctic fur seals were highest at 60 – 120 km from land and decreased sharply at distances beyond 150 km. This creates a overlap with krill fisheries, which almost entirely operate within 100 km of land (Trathan et al. 1998a). This study operated on a finer scale, concentrating on the distribution of predators up to 100 km from land. Within this region, the patterns in distribution of Antarctic fur seals is similar to those found for krill by Trathan et al. (2003), where krill densities were found to be higher over the shelf compared with off shelf, and were highest at the shelf edge.

Though we can measure the spatial characteristics of foraging, krill distribution and fishing effort, understanding the potential for competition is

dependent upon quantifying of the demand for krill by predators and fisheries and by understanding the availability and replenishment rates of the krill population. See Chapter Five for an approach to this.

#### ***4.4.2 Relationships between replicate surveys***

Though significant relationships were found between the distributions of seals along transects from the replicate surveys, these were atypical and it should be considered that no consistently significant relationship existed. South Georgia is a region renowned for its high heterogeneity in oceanography and krill distribution. Close temporal replication of the transect on the same or next day may yield stronger correlation results and it would be very interesting to investigate the temporal scales over which relationships do exist (Everson and Murphy 1987).

#### ***4.4.3 Correlation between transect and telemetry derived distributions along transects***

The comparison of telemetry and transect derived distributions along transect lines found significant relationships for distribution during the second, but not within the first survey. As with the relationship between the two replicate transects, this inconsistency in correlation is probably due to the highly heterogeneous nature of the system. The telemetry data provides a composite distribution that represents spatial usage over the survey period whilst the transect data represented a temporal snapshot, a sub-set of the telemetry data.

#### ***4.4.4 The relationship between krill and seal distribution***

The relationship between Antarctic fur seals and krill was examined with krill densities to two depths horizons, to 50 m (a depth chosen to represent the krill available to seals) and to 250 m (the general depth over the shelf and often considered when estimating krill density). A strong relationship was found when considered to 250 m depth, but the same relationship was not present when considered for krill to 50 m. This lack of relationship with krill to 50 m is more likely due to difficulties associated with measuring krill density near the surface than reflecting a different predator-prey relationship. The acoustic instrumentation used within this cruise was hull mounted, at six meters below the surface, this combined with surface noise associated with ship movement and wave action makes accurate estimates of krill in the surface waters problematic. Future surveys may do well to use some surface mounted or side-scan acoustics.

Correlation strengths of seal distribution along transects increased with spatial scale. This is in agreement with studies of other pelagic predators foraging on clustered prey (Schneider and Duffy 1985; Schneider and Piatt 1986; Hunt and Schneider 1987; Rose and Leggett 1990; Hunt et al. 1992; Wright and Begg 1997; Ritchie 1998; Mehlum 1999; Reid 2001b; Davoren et al. 2002). Other studies have also found relationships between predators and prey to be inconsistent, with varying results between different sampling days (Schneider and Piatt 1986; Burger et al. 2004), seasons (Davoren et al. 2002) and years (Wright and Begg 1997).

#### ***4.4.5 The influence of physical factors on the distribution of Antarctic fur seals, a comparison of two surfaces***

Trying to find fine scale relationships between the distributions of two data sets that are so dependent upon spatially dynamic processes is very difficult. Trathan et al (2003) investigated links between krill density and bathymetry within the same region as this study and found fine-scale relationships, with the shelf break region, and waters over the shelf having consistently higher krill biomass, particularly between depths of 250 and 750 m.

Using models of the physical habitat preferences of Antarctic fur seals (one model based on the distribution determined by transect and the other on telemetry derived distribution), allowed us to examine the variability of the system and investigate if the underlying factors driving the distributions were similar. Though the models had a low overall ability to explain variability in seal distribution, when the two modelled distributions were compared, very strong significant relationships were found.

We do not know what proportion of the population at-sea around South Georgia are non-central place foraging animals, we do know however that they don't all come from the Bird Island population and that the population around South Georgia also includes juveniles, non-breeding females and males. It therefore seems reasonable to conclude that the factors influencing seal foraging are more resource-dependent, and potentially reflect those that influence prey distribution, rather than state-dependent. i.e. it doesn't matter if you're a male, female, young or old, animals still have to



forage where the krill exist. This therefore means that it is also reasonable to use our understanding of seal behaviour from tracking females from Bird Island as a proxy for the whole population and as a good indication of overall resource distribution and availability. This is especially important as a large proportion of the foraging population are juvenile animals, and were estimated by Boyd (2002a) to account for 62% of Antarctic fur seal demand for krill making it essential to better understand this portion of the population.

#### ***4.4.6 For further consideration***

The findings of this study have further implications for our understanding of the South Georgia ecosystem. With the knowledge that telemetry can give a representative picture of seal distribution, and that seal distribution is representative of krill distribution, one can use the British Antarctic Survey historical telemetry records to look at patterns in krill distribution over the past decade.

Such an analysis is of key importance in determining the nature of and extent of competition for krill at South Georgia. If there is strong intra-specific competition, then given the high numbers of central placed foraging animals at South Georgia we may expect those without the same constraints to forage further from the island. The results of this study suggest that there is little difference in foraging location between constrained and less-constrained animals. This could suggest that there is sufficient optimal foraging habitat within range of the limits imposed by central placed foraging for all seals to the extent that the extra cost in travelling beyond the range of constrained population may not be necessary.

## CHAPTER FIVE

### **Tipping the scales, the spatial demand and supply balance of krill to the northwest of South Georgia, summer 2002**

#### **5.1 INTRODUCTION**

Understanding the balance of the supply and demand between predators and their prey is a fundamental of ecology (Odum 1959; Barbosa and Castellanos 2005) and the relationships between marine top predators and prey no less so (Cairns 1987; Levin 1990; Estes et al. 1998; Tasker et al. 2000; Harwood 2001; Brooke 2004; Hooker and Gerber 2004; Williams et al. 2004; Witteveen et al. 2006). In the South Georgia region large scale exploitation of krill predators especially seals and whales has lead to changes in the nature of the demand for Antarctic krill (*Euphausia superba*) (Harmer 1931; Hardy and Gunther 1935; Mattsson 1942; Mori and Butterworth 2005). That coupled with inherent variability in the krill population itself, and potential expansion of krill fisheries, means the need to understand this predator-prey balance has never been greater (Murphy et al. 1996; Brierley et al. 1997; Trathan et al. 1998a; Everson et al. 2000; Reid and Croxall 2001; Trathan et al. 2003; Hewitt et al. 2004b; Reid et al. 2005): Thus the demand for and availability of Antarctic krill to its predators has being the subject of extensive research and debate (Laws 1977; Croxall et al. 1984; Croll and Tershy 1998; Thomson et al. 2000; Barlow et al. 2002; Boyd 2002a; Alonzo

et al. 2003b; Fraser and Hofmann 2003; Mori and Butterworth 2004; Reid et al. 2004)

The availability of krill at South Georgia varies between years and years of particularly low abundance can have a pronounced negative effect on the reproductive success of krill dependent species (Agnew 1997; Brierley et al. 1997; Murphy et al. 1998; Croxall et al. 1999; Reid et al. 1999a; Reid and Croxall 2001; Brierley et al. 2002; Trathan et al. 2003; Reid et al. 2005; Trathan et al. 2006). The extent of competition between these species of krill-consuming predators is difficult to quantify. Different predator species show varying degrees of reproductive success in different years, some species such as Antarctic fur seals (*Arctocephalus gazella*) change diet whereas other species continue to feed on krill e.g. macaroni penguins (*Eudyptes chrysolophus*) (McCafferty et al. 1998b; Croxall et al. 1999; Barlow et al. 2002; Trathan and Croxall 2004; Reid et al. 2005).

Antarctic fur seals forage in both the on-shelf and off-shelf regions (Chapter Four; Staniland and Boyd 2003; Staniland et al. 2004). However, when foraging from Bird Island they tend to travel out to the northwest of the island rather than to the nearest shelf break region. It is the shelf break region where krill density is thought to be highest (Trathan et al. 2003); and this is also the area targeted by the krill fishery (Murphy et al. 1996; Trathan et al. 1998a). It is thought that though a seal may set out in the direction of predetermined foraging area, the actual feeding area is a response to the krill distribution they encounter whilst swimming away from the island i.e. seals sample the water column en-route and will forage when a suitable prey patch is found (Staniland and Boyd 2003). No difference has been found in the

profitability of on-shelf or off-shelf foraging trips (Staniland et al. 2004). It seems possible that krill may be more predictable or profitable off-shore, whilst increased competition or lower patch density/predictability on-shelf may reduce profitability, the lower swimming effort or time investment required makes up for this (Hughes 1980).

Previous estimates have been made of the predator demand for krill in the South Georgia region but they have usually not been area specific and generalised to the region (Boyd and Croxall 1996b; Barlow et al. 2002; Boyd 2002b; Boyd 2002a; Hewitt et al. 2004c).

Duffy and Schneider (1994) highlighted that fine-scale temporal comparisons of predator demand with prey availability can aid in predicting and mitigating potential conflicts between predators and commercial fisheries. The importance of understanding krill consumption at smaller scales has been recognised in the development of management approaches to the krill fishery. There is a great need to understand these by balancing these predator-prey relationships at fine scales (Hewitt et al. 2004c). The process of allocating krill catch limits to spatially specific and small-scale management units recognise the need to take into account the balance of predator consumption in each area in order to avoid localised negative effects on predator populations (Hewitt et al. 2004c).

In 2002 the British Antarctic Survey undertook an intensive, multidisciplinary cruise in a study region to the northwest of South Georgia, known as the Western Core Box (WCB). The aim of the cruise was to quantify krill biomass, import, growth, export and mortality through the study region, see Figure 5.1. As part of this process it was necessary to quantify the

role of krill predators in this ‘krill-flux model’. There are many krill predator species at South Georgia, however, this study is focused on some of the most significant land-based species; Antarctic fur seals (*Arctocephalus gazella*), macaroni penguins (*Eudyptes chrysolophus*), gentoo penguins (*Pygoscelis papua*) and Antarctic prions (*Pachyptila desolata*). As these species are constrained to return to land to feed their offspring during the period, December to March, they represent the group with the greatest demand for krill within their restricted foraging ranges. Other species considered significant but for which we have limited data are baleen whales (Reilly et al. 2004) and fin fish (Kock 1985).

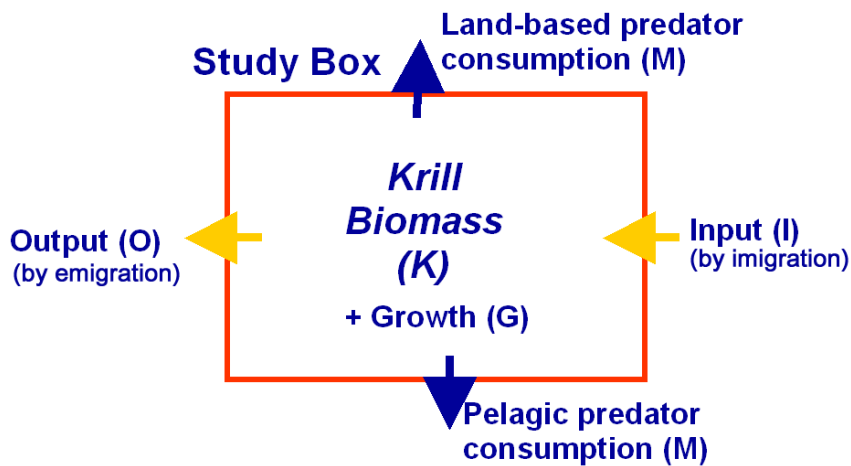


Figure 5.1. Functional diagram of the key processes involved in the krill flux balance.

There is some evidence that predators may not feed on all parts of the krill population (Hill et al. 1996; Reid et al. 1996; Croxall et al. 1997; Murphy and Reid 2001). Thus it is important to identify which parts of the krill population support predator demand and what proportion of the available krill biomass this represents.

This thesis has developed methods for understanding the fine scale distribution and density of krill predators within the WCB. This chapter builds on understanding from previous chapters to quantify the total, length-specific and spatially specific, demand for krill by the main land breeding krill predators within this study region, and relates this to the available krill population.

## **5.2 METHODS**

These methods have three component parts: (1) modelling the overall, spatially explicit, demand for krill for each predator in the WCB; (2) breaking down this overall demand to the specific length-frequency categories required for each predator; and (3) relating this to the spatial distribution and length frequency of the available prey population.

### ***5.2.1 Modelling prey demand***

The model has three component parts consisting of: (i) estimation of individual energy components (energetic component); (ii) estimation of food requirements (diet component); and (iii) estimation of population size and structure (population component).

#### ***Incorporating uncertainty***

The model includes a number of variables that have some degree of uncertainty, for this reason variance throughout the model was incorporated using Monte Carlo simulation techniques (Manly 1991). This allows the incorporation of the uncertainty at each level of the model into the final estimate. In each run of the model parameter values were randomly selected

from assigned probability distributions that best described their uncertainty. Thus, each run of the model produced one estimate of krill demand according to a particular set of parameters, and multiple runs of the model, each with a different set of parameters, produced a distribution of estimated krill demand.

One of two types of sampling distribution, uniform and normal, were applied depending upon the assumed nature of the real distribution of each variable. Normal sampling distributions were defined by a mean and standard deviation (e.g.  $0.8 \pm 0.3$ ). Where distributions were less well understood or were non-normal, uniform sampling distributions were used; these were defined by their plausible upper and lower limits (e.g. 0.6 to 0.9).

***(i) Energetic component***

Gross energy requirements were calculated for each demographic class of animal, defined by age, sex and state (dependent offspring/non-breeding/breeding) at the time of the survey (considered to be the 21/01/2002). Energetic models took a different form dependent upon the nature of the empirical data available.

***Antarctic fur seals***

The model for Antarctic fur seals was based on basal metabolic rates with specific activity multipliers. This was of the form:

$$G = \frac{P + (B * A)}{1 - F} \quad \text{Equation 5.1}$$

Where  $G$  is gross energy requirement,  $P$  is production,  $B$  is basal metabolism,  $A$  is an activity metabolic multiplier and  $F$  is the proportion of energy lost as waste in faeces and urine. These values were all taken from the literature, and are described below.

Boyd et al. (2002), found the Basal Metabolic Rate (BMR) of Antarctic fur seals to be consistent with the allometric relationships to mass ( $M$ ) described by Kleiber (1975) and to that specific for marine mammals described by Lavigne et al. (1986), such that  $B$  was estimated as  $B = 293M^{0.75}$  where  $B$  is in  $\text{kJ day}^{-1}$  and  $M$  is in  $\text{kg}$ . The influence of activity on the metabolic rates of Antarctic fur seals has been determined empirically and were defined as ashore (Costa & Trillmich, 1988) or at sea (Costa et al., 1989; Kleiber, 1975). These gave metabolic rates that were applied as multipliers of BMR for each activity. For time at sea ( $s$ ) this was  $s = 4.5 (\pm \text{SD } 0.3)$  and for time ashore ( $a$ )  $a = 3.0 (\pm \text{SD } 0.3)$  with a uniform error distribution. Antarctic fur seal activity budgets were defined as the proportion of time ashore ( $t_a$ ) and the time at sea ( $t_s$ ). For lactating females  $t_s = 0.8 (\pm \text{SD } 0.16)$ , this was based on empirical data and were the same as those used by Boyd (2002b). Juvenile seals were thought to still forage in the area and so still be part of the study population, yet without the same reason to come ashore, the proportion of their time at spent at sea was increased such that  $t_s = 0.9 (\pm \text{SD } 0.1)$ .

### ***Macaroni penguins***

Macaroni penguin energy requirements were based on Field Metabolic Rates (FMR) recorded at the time of the study from Bird Island (Green et al., Unpublished data). FMR was  $1085 \text{ kJ kg day}^{-1} (\pm \text{SD } 114)$  and was estimated from 12 birds (male and female) who's FMR was recorded between 15/01/02 and 27/01/02. At the time of the study macaroni penguins were at the mid point of the transition between brood guard and the start of chick rearing. Upon moving into chick rearing, adult energy requirements increase significantly (Boyd, 2002b; Croxall, 1984; Davis et al., 1989).



Macaroni chick requirements were also measured at the time of the study and were based on regurgitated samples collected as chicks were fed. Thus this was not added to the parents energy requirements as production but was added as a daily required wet krill mass. The average wet krill mass per regurgitate ( $K_r$ ) around the time of the cruise was 386 g ( $n=36 \pm \text{SD } 249$ ) (British Antarctic Survey, unpublished data), and was consistent with meal masses described by Barlow and Croxall (2002a).  $K_r$  was then multiplied by the average number of feed the chicks received per day ( $\bar{f}_i$ ), (derived from Barlow and Croxall (2002a) where  $\bar{f}_i = 1.09 (\pm \text{SD } 0.21)$ ) to give the daily requirements per chick  $C_k$ .

### ***Gentoo penguins***

For gentoo penguins, metabolic rate was calculated as an average over a longer time period using the average rates give by Bevan et al. (2002), as the standard deviation (SD) are derived from  $\log_e$  transformed data, the upper and lower SD are not equal, where the average FMR were 476 ( $\pm \text{SD } 58, 67$ ) kJ kg day<sup>-1</sup> during chick rearing and 688 ( $\pm \text{SD } 107, 126$ ) kJ kg day<sup>-1</sup> during brood guard. For penguins and prions both parents were assumed to equally provide food to the chick, and hence have the same activity budgets (Bevan et al., 2002).

As with macaroni penguins, gentoo chick requirements were also measured at the time of the study and were based on regurgitated stomach contents. Gentoo penguins are different to macaroni penguins in that they have two chicks. Here I multiply  $K_r$  by the foraging trip rate (i.e. the number of times an animal returns to shore per day) this is effectively the same as  $\bar{f}_i$  with macaroni penguins, and is applied in the same way. The average wet krill

mass per regurgitate ( $K_r$ ) around the time of the cruise was 747 g ( $n = 32$  SD = 389) (British Antarctic Survey, unpublished data). And  $\dot{f}_i$  was estimated as  $\dot{f}_i = 0.94$  ( $\pm$  SD 0.75, 1.07) during crèche and  $\dot{f}_i = 0.97$  ( $\pm$ SD 0.82, 1.20) during brood guard (Williams & Rothery, 1990).

### ***Prions***

Prion metabolic rates were based upon those given by Taylor et al. (1997) where the average field metabolic rate was 391.0 ( $\pm$  SD 21.0) kJ kg day<sup>-1</sup>. The requirements of chicks were based on regurgitated meal mass ( $K_r$ ) and delivery rate ( $\dot{f}_i$ ) as described by (Reid et al., 1999b), this gave total daily requirements of wet food mass per chick to be 30 ( $\pm$  SE 1.4) g day<sup>-1</sup>.

### ***Other factors***

Faecal and urinary loss ( $F$ ) was represented as between 2 to 8% of gross energy loss for fur seals (Brody, 1945). Penguin and prion metabolic rates were expressed as field metabolic rate and so no explicit allowance was made for faecal and urinary losses.

Penguins and prions achieve their adult mass, or greater, at fledging and little energy is put into growth from there onwards, production ( $P$ ) from growth for was not included for these animals. Macaroni and gentoo penguins adults have been shown to lose mass over the chick rearing/brood guard period (Bevan et al., 2002; Davis et al., 1989). Fur seals grow throughout their lives (Payne, 1979) though it was assumed that at the time of the study, the pressure to maintain offspring would render the cost of growth to be insignificant relative overall metabolic rates associated with activity and so this was disregarded for the proportion of animals rearing offspring. For Antarctic fur seals without dependent offspring growth was included. This

was based upon the annual increase in mass at age, derived from Payne (1979) and were assumed to be equal over the year. Total body energy composition was based on values given by Arnould et al. (1996) and were estimated as adult females, 10.59 ( $\pm$  SD 0.30) Mj kg<sup>-1</sup>, and pups 8.24 ( $\pm$  SD 0.41) Mj kg<sup>-1</sup>.

**Table 5.1. Energetic parameters**

Parameter	Value	Error	Units and details	Source
<b>Antarctic fur seals</b>				
BMR	$293M^{0.75}$	-	$\text{kJ kg day}^{-1}$ , $M$ = mass in kg	(Boyd 2002a)
Metabolic multipliers				
At-sea ( $s$ )	4.5	$\pm$ SD 0.3	-	(Costa et al. 1989)
Ashore ( $a$ )	3.0	$\pm$ SD 0.3	-	(Costa and Trillmich 1988)
Adult proportion of time at-sea ( $t_s$ )	0.8	$\pm$ SD 0.16	-	(Boyd 2002a)
Non-breeder proportion of time at-sea ( $t_s$ )	0.9	$\pm$ SD 0.01	-	(Boyd 2002a)
Faecal and urinary loss	2 to 8%		% of gross energy loss $\text{day}^{-1}$	(Brody 1945)
<b>Macaroni penguins</b>				
Adult FMR	1085	$\pm$ SD 114	$\text{kJ kg day}^{-1}$	(Green et al. 2005a)
Wet krill mass per regurgitate ( $K_r$ )	386	$\pm$ SD 249	$\text{g day}^{-1}$	BAS, unpublished data
Number of feeds per day ( $\bar{f}_i$ )	1.09	$\pm$ SD 0.21	$\text{day}^{-1}$	(Barlow and Croxall 2002a)
<b>Gentoo penguins</b>				
Adult FMR (chick rearing)	476	$\pm$ 95% CI 418, 543	$\text{kJ kg day}^{-1}$	(Bevan et al. 2002)
Adult FMR (brood guard)	688	$\pm$ 95% CI 581, 814	$\text{kJ kg day}^{-1}$	(Bevan et al. 2002)
Wet krill mass per regurgitate ( $K_r$ )	747	$\pm$ SD 389	$\text{g day}^{-1}$	BAS, unpublished data
Number of feeds per day $^{-1}$ ( $\bar{f}_i$ ) (chick rearing)	0.94	$\pm$ 0.94, 1.07	$\text{day}^{-1}$	(Williams and Rothery 1990)
Number of feeds per day $^{-1}$ ( $\bar{f}_i$ ) (brood guard)	0.97	$\pm$ 0.82, 1.20	$\text{day}^{-1}$	(Williams and Rothery 1990)
<b>Antarctic prions</b>				
Adult FMR	391	$\pm$ SD 21	$\text{kJ kg day}^{-1}$	(Taylor et al. 1997)
Wet krill mass per chick day $^{-1}$	30	$\pm$ SE 1.4	$\text{g day}^{-1}$	(Reid et al. 1999b)



**(ii) Diet component**

For Antarctic fur seals it was assumed that krill made up 90% ( $\pm$  SD 5%) of the diet by wet mass with the remainder made up by finfish. The diet composition of macaroni penguins was estimated at 80% ( $\pm$  SD 20%  $n = 40$ ) krill by wet mass and for 79% ( $\pm$  SD 21%  $n = 32$ ) by wet mass for gentoo penguins based on samples taken at Bird Island during the period of the cruise (British Antarctic Survey, unpublished data). The diet of prions, based on regurgitate fed to chicks, was assumed to consist of 68% ( $\pm$  SD 28%) krill by wet mass based on samples taken at BI during the period of the cruise (British Antarctic Survey, unpublished data). The remaining diet for penguins was made up of 60% fish and 40% mixed crustaceans, and 100% mixed crustaceans for prions. For all ages and sexes, diet was assumed to be consistent. It is likely that the fish consumed by Antarctic fur seals also contained krill in their own stomachs, however this secondary consumption was not considered in this study.

Digestive efficiency is the gross energy intake less the energy lost as faeces expressed as a proportion of the gross energy intake. As digestive inefficiencies were prey specific, they were incorporated into the model by subtracting them from the total prey energy values rather than in the energetic component of the model. Due to high consistency amongst species, the same digestive inefficiency values were used for all predator species and were taken from Boyd (2002a). These were 0.84 for krill and 0.87 for fish, both having a  $\pm 0.02$  error with uniform probability distribution. The total energy content of wet weight prey was considered to be 4.6 kJ g<sup>-1</sup> for krill (Clarke 1984), 4.6 kJ

$\text{g}^{-1}$  for mixed crustaceans and  $5 \text{ kJ g}^{-1}$  for fin fish species (Cherel and Ridoux 1992; Boyd 2002a).

### (iii) *Population component*

Each individual in the population was represented by the proportion of its demographic; defined by age, sex and reproductive state, making up the total population believed to be in the study box at the time of the survey.

For Antarctic fur seals the proportion of each demographic class was obtained from those given by Boyd (2002a) and associated mass at age was taken from Payne (1979); these values are given in Table 5.2.

**Table 5.2. Mass at age (kg) for different age classes of Antarctic fur seals, values for juvenile and adults are for females. Taken from Payne (1978).**

Age	Mean (kg)	SD	Range	Frequency
Male weaning 0	17.0	2.60	12.3 - 22.4	-
Female weaning 0	13.5	2.05	8.8 - 17.5	-
1	16.0	0.66	14.8 - 16.9	0.1755
2	21.0	2.92	18.3 - 24.0	0.1561
3	25.4	6.18	21.8 - 29.7	0.1384
4	28.7	4.06	22.0 - 38.5	0.1053
5	31.2	3.24	22.9 - 37.2	0.0859
6	31.8	4.03	24.9 - 42.9	0.0704
7	32.6	4.43	19.5 - 41.5	0.0581
8	34.1	5.10	23.4 - 44.0	0.0487
9	34.5	5.44	23.6 - 42.9	0.0405
10	35.6	7.27	27.7 - 50.8	0.032
>11	38.2	6.2	27.0 - 49.2	0.089

Adult macaroni penguin mass was estimated as 4.2 kg ( $\pm$  SD 0.4) (Boyd 2002a) and adult gentoo mass was estimated at 6.3 kg ( $\pm$  SD 0.2) (Bevan et al. 2002). Adult prion mass was estimated as 149 g ( $\pm$  SD 30) (Taylor et al. 1997). All these birds reach adult body mass (or greater) at fledging.

Previous models of prey demand by seabirds or seals have generally been based on a whole population (Boyd 2002a; Winship et al. 2002), where

demographic information and thus representation of individual energy demands, are based on census of the haul-out site or breeding area. This model was different in that it was concerned only with those animals using a predetermined area of ocean; this meant that the energy requirements of dependent offspring had to be added to the overall requirement of their providing parent.

For fur seals,  $G$  was calculated for dependent pups and was incorporated into  $P$  in the energetic model of the providing parent (Equation 5.1). If breeding failure occurs, the mother returns to sea very soon afterwards, and was assumed to return to winter behaviour spending all of her time at sea. Boyd et al. (1998) found that female seals sometimes remain in the South Georgia region outside the breeding season. The proportion of adult (three years or greater) females with dependent pups at the time of survey was estimated at between 0.75 to 0.95 with a uniform distribution.

It is thought that at the time of the survey most male Antarctic fur seals have already left the region (Boyd et al. 1998). For the purposes of this study, juvenile males Antarctic fur seals were assumed to mimic the behaviour of adults. This, combined with the fact that few male animals were noted at sea (see Chapter Two) meant that we assumed the population of the study box to be all female. We assumed other species to be equally represented by sex.

For seabirds we assumed that the population of the study box would represent the overall demographics of the population, as such the proportion of the population with dependent chicks had to be estimated for each species. For macaroni penguins and prions survival rates and hence the proportion of



breeding adults in the population is relatively unknown. For gentoo penguins, the proportion of breeders within the population was estimated to be between 0.5 and 0.7 (British Antarctic Survey, unpublished data) and the same values were applied for prions. For macaroni penguins the age of first breeding is much older than for gentoo penguins (Williams 1995) and the proportion of breeders within the population was estimated to be lower than that for gentoo penguins. The proportion of breeders ( $P_b$ ) in the population was based on a simple population simulation model structured as:

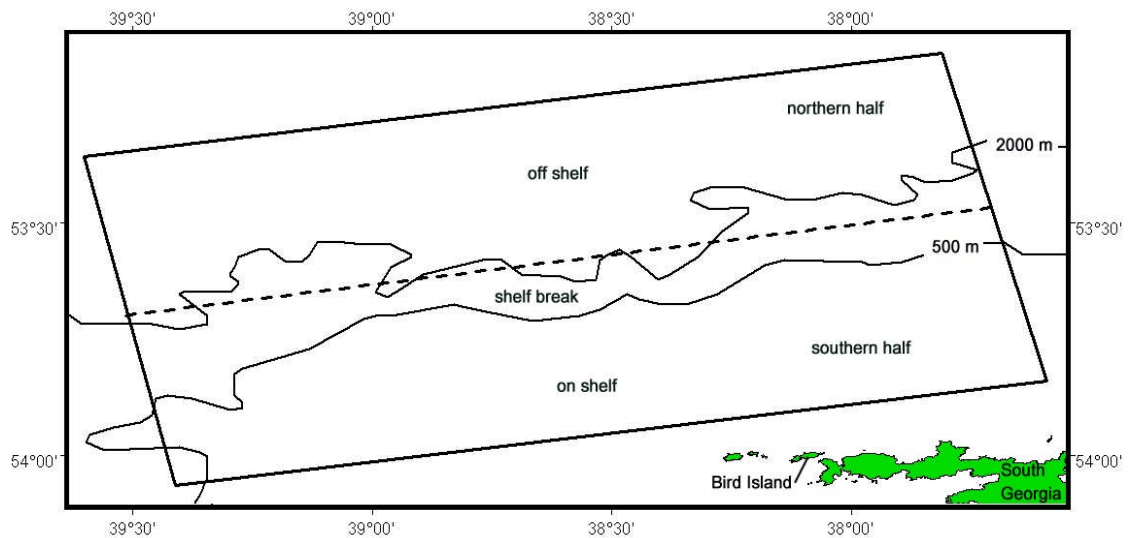
$$n_a = n_{a-1} * s_{a-1} \quad \text{Equation 5.2}$$

and

$$Pb = \left( \frac{n_a}{\sum n_{a1-31}} \right) * f_a \quad \text{Equation 5.3}$$

Where: the number of animals at year  $a = n_a$ , first year survival ( $s_{a1}$ ) = 0.468 ( $\pm$  SD 0.013) (British Antarctic Survey, unpublished data), adult survival rate ( $s_{a2-34}$ ) = 0.8 ( $\pm$  SD 0.03), age at first breeding = 5.5 (Williams 1995) thus annual fecundity rate ( $f_a$ ) for animals  $< 5.5$  years of age = 0 and an annual fecundity rate ( $f_a$ ); for adult birds (the proportion of birds breeding in consecutive years) ( $a > 5.5$ ) = 0.715 ( $\pm$  SD 0.07) (Williams and Rodwell 1992). For the proportion of the population breeding, the total daily demand of the chick was added. Provisioning rate of the adults is known to differ between the sexes, especially for macaroni penguins (Barlow and Croxall 2002a). As we are interested in the demand of the box for one day this seemed a reasonable alternative to splitting the demands of the chick(s) between the two parents.

The average density and total population of the study box was determined by at-sea line transect survey and results are presented in Table 5.3. The methods used to determine density values and their associated error for each species are discussed in Chapter Two for Antarctic fur seals and Chapter Three for penguins and prions. These values were available for fine scale spatially specific regions and so the demand for krill was broken down into regions of the study box, such that density and demand was divided by depth (0-500 m, 500 – 2000 m and deeper than 2000 m) and into the northern and southern halves of the study region, see Figure 5.2. Due to the high number of zeros in these data there is a highly negatively skewed distribution, with the result that the sum of animals, calculated from the arithmetic mean, in the sub-areas is not equal to that of the whole and is consistently negatively biased. They do however remain valuable for illustrative purposes.



**Figure 5.2.** Map showing Western Core Box study area with spatial divisions based on depth (0-500 m, 500 – 2000 m and deeper than 2000 m) and northern and southern sectors of the area.

**Table 5.3. Predator density estimates (animals km<sup>-2</sup>) within different sectors of the study area. As determined by line transect survey in January 2001. Full description of methods and applied multipliers can found in Chapters Two and Three.**

<b>Area</b>	<b>Density</b>	<b>% CV</b>	<b>95% CI</b>	<b>In area (individuals)</b>
<b>Antarctic fur seal density</b>				
Whole box	39.64	12.94	30.06, 49.23	404461
On-shelf	41.78	17.87	36.34, 47.23	169468
Shelf break	33.30	12.75	15.06, 51.54	69038
Off-shelf	44.09	19.29	26.01, 62.18	200050
Southern box	40.76	12.44	35.80, 45.73	216843
Northern box	40.89	58.22	25.58, 56.20	217535
<b>Macaroni penguin density</b>				
Whole box	4.39	20.88	1.94, 7.72	46656
On-shelf	7.93	27.66	3.53, 14.03	32166
Shelf break	0.00	-	-	0
Off-shelf	0.11	1.08	0, 0.66	499
Southern box	7.00	26.16	3.14, 12.31	37213
Northern box	0.08	0.90	0, 0.17	399
<b>Gentoo penguin density</b>				
Whole box	4.64	22.82	2.13, 8.11	49316
On-shelf	8.42	30.28	3.88, 14.80	34153
Shelf break	0.00	-	-	0
Off-shelf	0.00	-	-	0
Southern box	7.44	28.57	3.45, 12.99	39554
Northern box	0.00	-	-	0
<b>Prion density</b>				
Whole box	27.01	69.09	13.97, 40.05	287386
On-shelf	47.04	52.80	23.89, 70.90	190804
Shelf break	2.01	38.48	0.75, 3.27	4167
Off-shelf	1.87	28.98	1.13, 2.61	8485
Southern box	42.01	56.14	21.18, 62.84	223493
Northern box	2.17	32.23	1.37, 2.97	11544

### ***Sensitivity analysis***

The contribution to the total variance (the variance estimated when all parameters are stochastically incorporated) from each of the input variables was assessed by sensitivity analysis of the model. This was carried out by systematically incorporating the uncertainty belonging to one variable whilst holding the others constant at their deterministic values. The model was then run 1000 times and the proportion of the total variance was assessed.

Also investigated was degree of influence that each parameter had on the model results. i.e. the effect of independently varying each of the input variables on the final output value. To do this the average value of one variable was increased or decreased by 10% whilst the others were again held at their deterministic values.

#### ***5.2.2 Krill density***

Krill density was measured acoustically at the same time as counts of predators from the survey vessel, to depths of both 50 and 250m. Acoustic determinations were made using a Simrad EK500 echosounder operating hull-mounted 38, 120 and 200 kHz transducers. Synchronous pulses from all transducers were transmitted every 2.5 seconds at a nominal survey speed of 10 knots. 120 kHz Sv values identified as originating from krill targets were converted to mean krill densities ( $S_v$  = acoustic volume backscatter coefficient), see Brierley & Watkins (1995). Transect krill densities were weighted by transect length and averaged within the survey area to determine overall krill densities and weighted variances in the same procedure described in Chapter Two and used for fur seals.

Overall densities were then divided into the same depth regions described for predators, the results of which are shown in Table 5.4.

**Table 5.4. Krill population density (tonnes km<sup>-2</sup>) within the study area January 2001.**

Area	Krill density			
	Density	% CV	± 95% CI	In area (tonnes)
Whole box	54.49	41.98	0, 110610	579773
On-shelf	80.87	46.82	0, 168050	328000
Shelf break	93.92	61.31	0, 385650	276500
Off-shelf	21.05	128.20	0, 79005	95500
Southern box	87.30	39.75	4070, 182260	465000
Northern box	23.70	121.40	0, 75690	126000

### 5.2.3 Other predators

A report by Hewitt et al. (2004c) considered other significant krill predators in the South Georgia region to be fish (Kock 1985) and baleen whales (Reilly et al. 2004) and provided an estimates of an annual consumption rate of 9070.9 tonnes of krill over an area of 42800 km<sup>2</sup> covering the main predator foraging areas within approximately 130 km of the coast of the western half of South Georgia. Hewitt's estimates of demand for krill within this study were scaled to the area of the WCB (10640 km<sup>2</sup>) and to daily rather than annual estimates see Table 5.5.

**Table 5.5. Predicted daily krill demand (tonnes day<sup>-1</sup>) by dominant krill predators within the WCB adjusted from Hewitt et al. (2004c), see text for details.**

<b>Predator</b>	<b>Demand (tonnes)</b>
Antarctic fur seals	475.34
Penguins	5297.60
Whales	131.33
Fish	290.80

Subsequent analyses in this study are presented for Antarctic fur seals alone and then presented combined with other krill predators.

#### ***5.2.4 The supply and demand balance: Consumption rates***

The relationship between krill demand and availability was expressed as a consumption rate, the percentage of the total stock taken each day. This assumed no growth, no natural mortality, no additional predators and a closed population.

#### ***5.2.5 Length specific demand***

To optimise foraging profitability, predators often forage preferentially on prey of a certain size, which may not represent the size range of the prey population (Kaiser and Hughes 1993; Hughes and Seed 1995); Diet studies have found longer krill and gravid female krill to be more prevalent in the diet than in the krill population (Reid et al. 1996; Reid et al. 1999c). Smaller krill yield less energy return per krill, yet only taking the larger krill may be inefficient due to greater search time. It is also thought that larger, gravid females may have slower escape responses than smaller or male krill. Where such preference is shown, comparing predator demand with the whole prey population can be misleading as the predator requirement must be met by some fraction of the total prey population. Therefore it may be

appropriate to consider the demand as a relative consumption estimate within specific size classes of the prey population.

Concurrently to this study samples of krill length were obtained by other scientists using an Rectangular Midwater Trawl (RMT 8) following methods described by Hill et al. (1996). and total length (AT) of whole krill, from the front of the eye to the tip of the telson was measured (Lockyer 1973; Morris et al. 1988).

Krill were also measured in the diet of penguins and seals from adults returning to feed offspring at Bird Island during the period of the cruise. Samples from penguins were collected by stomach lavage (Wilson 1984) using standard methods developed by the CCAMLR Ecosystem Monitoring Program (CEMP) (CCAMLR 1995). Lavage involves inducing regurgitation by filling the stomach with warmed water (Wilson 1984). Antarctic prion diet composition was taken from the literature (Croxall et al. 1997). Diet samples from Antarctic fur seals were collected by enema from adult females as they returned to Bird Island, for methods see Staniland et al. (2003). The total length of krill from penguins was estimated using the Removed Carapace Length (RCL) following the methods and using the maturity/sex specific equations in Hill (1996) and Reid and Measures (1998). These samples were taken by the team stationed on Bird Island.

Length frequency distributions of krill in the diet of fish were taken from Kock et al. (1994) where values were based on the diet of mackerel ice fish (*Champsocephalus gunnari*), this was considered to be representative of other fish species.

Baleen whales were considered to be non-selective when taking krill and the length frequency distribution of krill in the diet of baleen whales was considered to be the same as the length frequency distribution of the krill population (Nemoto 1966; Brown 1968; Mackintosh 1974; Kawamura 1994).

Mass at length of krill was estimated using generalised values and applied the methods described by Morris et al. (1988). Here the relationship between length and mass was described by the power relationship:

$$W = aL^b \quad \text{Equation 5.4}$$

Where  $W$  = weight (g),  $L$  = length (mm),  $a = 3.39(\times 10^{-6})$  = length coefficient and the exponent ( $b$ ) was equal to 3.23. These values are for wet weight krill for AT length measurements (mm) (Morris et al. 1988).

### ***Krill growth***

Krill growth rates have been the focus of much research with rates varying greatly and associated with length (Atkinson et al. 2006), time of year (Buchholz et al. 1989; Reid 2001a), reproductive state (Buchholz et al. 1996), water temperature (Arnold et al. 2004; Atkinson et al. 2006) and food availability (Astheimer et al. 1985; Reid 2002). During this study krill growth rates for the population of the study box were measured from net caught krill onboard the RRS James Clark Ross ( $n = 773$ ) (Atkinson et al. 2006). Here rates are based on averaged growth rates ( $\text{mm day}^{-1}$ ) specific to each length class of krill. For direct comparison to biomass predation rates these were adjusted to a percentage growth in wet biomass ( $\text{g day}^{-1}$ ) for each length category, for this reason krill in the 30 – 36 mm length classes were allocated the growth rate of  $1.2 \text{ mm day}^{-1}$ .



### ***5.2.6 Demand supply balance in previous years***

During the season of this study (2002) there was no evidence that fur seals had difficulty finding sufficient food. However, in previous years, low estimates of krill density within the region have coincided with higher than average breeding failure in krill dependent predators (Croxall et al. 1999; Barlow et al. 2002; Brierley et al. 2002; Reid 2002; Trathan et al. 2006). Based on demand and growth estimates from this study, we investigated the supply demand balance with the estimated krill population in the years 1991 through to 2001. This part of the analysis was carried out for the demand of Antarctic fur seals only.

## **5.3 RESULTS**

### ***5.3.1 Individual prey requirements***

Modelled prey requirements and their associated standard errors stabilised by 1000 runs of the model are given in Figure 5.3. The average Antarctic fur seal in the study box was estimated to require 4.57 ( $\pm$  SE 0.37) kg of krill day<sup>-1</sup> (Table 5.6). The individual demand for krill by penguins was similar for macaroni and gentoo penguins 1.18, ( $\pm$  SE 0.36) for macaroni and 1.20 ( $\pm$  SE 0.18) kg of krill day<sup>-1</sup> for gentoo penguins. As expected the daily krill requirements of prions was much lower than other species (0.032,  $\pm$  SE 0.01) kg of krill day<sup>-1</sup>.

**Table 5.6. Individual demand for krill ( $\text{kg day}^{-1}$ ) for animals within the Western Core Box study area. Estimates are for energy requirements specific to the period January 13<sup>th</sup> to 23<sup>rd</sup>.**

<b>Species</b>	<b>Mean</b>	<b>SE</b>	<b>95% CI</b>
Antarctic fur seal	4.57	0.37	3.84, 5.30
Macaroni penguin	1.18	0.36	0.47, 1.89
Gentoo penguin	1.20	0.18	0.85, 1.55
Antarctic prion	0.032	0.01	0.012, 0.052

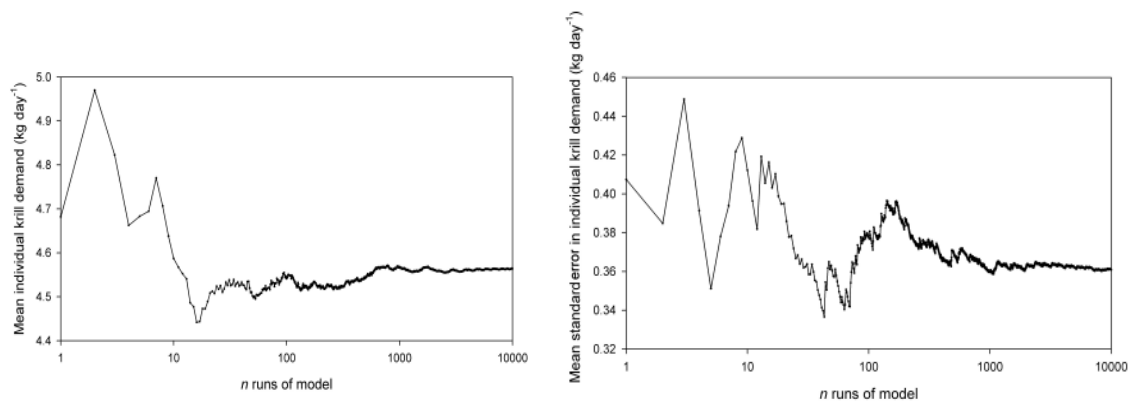
### ***5.3.2 Individual demand sensitivity analysis***

The results of sensitivity analysis are a function of the extent of the parameter variation weighted by the degree of influence that parameter has on the final value i.e. a parameter may have a large variance, yet be of little consequence to the model results, whilst another with lower variance may have a much larger influence on model results. Consequently, overall sensitivity is best represented by the delta change in population mean resulting from a change in the input parameter.

All principle components of the model; metabolic rate, prey energy values, digestive efficiencies and predator population size influenced the model outcome by a similar value to the change in their input values. Changes to the population composition, and proportion of krill in the diet had little influence on final values and these also accounted for a very low portion of total variance. Population size accounted for most of the variance in demand estimates, 78% for Antarctic fur seals (see Table 5.7)

**Table 5.7.** Variation in food consumption by female Antarctic fur seals associated with each variable, when present in the model as the only variable with uncertainty, expressed as a proportion of the total variance in food consumption. Also shown is the sensitivity of mean food consumption to a 10% change in the average value of the input variables. A negative value indicates when the change in food consumption was opposite to the direction of change in the value of the variable. Analysis was performed using Monte Carlo simulation (1000 runs). Mean and standard errors of the source population are from those values going into the model and are averaged over 1000 runs.

Variable(s) in which uncertainty was incorporated	CV (%) of parameter	Proportion of total model variance explained	Sensitivity ( $\Delta\%$ )
Activity-specific metabolic rate	6.61	0.073	10.082
Proportion of females with pups	7.29	0.007	-0.087
Faecal and urinary loss	1.90	0.018	10.059
Age specific mass	7.41	0.062	7.278
Prey energy content	3.06	0.040	9.115
Proportion of krill in diet	3.44	<0.001	0.999
Digestive efficiency	1.70	0.013	11.103
Population size	12.94	0.785	10.116



**Figure 5.3.** Estimated individual Antarctic fur seal demand for krill ( $\text{kg day}^{-1}$ ) and its associated standard error averaged over 1 to 10000 runs of the simulation model.

### 5.3.3 Overall demand

The total daily demand for krill by Antarctic fur seals for the WCB was  $1940 (\pm 95\% \text{ CI } 1381, 2499) \text{ tonnes day}^{-1}$ . For Antarctic fur seals, gentoo and macaroni penguins, prions, whales and fish combined, the total demand estimate was  $2580 \text{ tonnes day}^{-1}$ . Antarctic fur seals accounted for 75% of this

demand; macaroni and gentoo penguins took 2.5% and 3.3% respectively; prions took only 0.40%, fish took 12% and baleen whales 5% of the total daily demand (where whale and fish demand was taken from Hewitt et al. (2004c), see Table 5.5).

**Table 5.8. Predator demand within the Western Core Box (tonnes) based on 1000 iterations of the model. (For Table 5.8.e the demand for krill by baleen whales and fish is included in the total demand estimate. Knowledge of the distribution of demand for krill by these predators was not available and so their total consumption has been allocated to sub regions proportionate to the area of each region.)**

<b>Area</b>	<b>Demand (tonnes)</b>	<b>SE</b>	<b>95% CI</b>	<b>Demand (tonnes/km<sup>2</sup>)</b>
<b>(a) Antarctic fur seal</b>				
Whole box	1940.01	285.12	1381.17, 2498.85	0.182
On-shelf	819.77	171.94	482.77, 1156.77	0.202
Shelf break	385.69	64.53	259.21, 512.17	0.186
Off-shelf	845.69	49.10	749.45, 941.93	0.186
Southern box	1009.47	197.93	621.53, 1397.41	0.190
Northern box	807.07	123.19	565.62, 1048.52	0.152
<b>(b) Macaroni penguin</b>				
Whole box	63.61	267.54	0.00, 587.99	0.006
On-shelf	43.39	130.50	0.00, 299.17	0.011
Shelf break	0.00	-	-	0.000
Off-shelf	0.66	6.04	0.00, 12.50	<0.000
Southern box	45.78	173.18	0.00, 385.21	0.009
Northern box	0.61	6.05	0.00, 12.47	<0.000
<b>(c) Gentoo penguin</b>				
Whole box	82.17	292.52	0.00, 655.51	0.008
On-shelf	43.90	116.32	0.00, 271.89	0.011
Shelf break	0.00	-	-	0.000
Off-shelf	0.00	-	-	0.000
Southern box	48.39	151.17	0.00, 344.68	0.009
Northern box	0.00	-	-	0.000
<b>(d) Prion demand</b>				
Whole box	8.79	10.75	0.00, 29.86	0.001
On-shelf	6.25	7.47	0.00, 20.89	0.002
Shelf break	0.13	0.15	0.00, 0.42	<0.000
Off-shelf	0.26	0.32	0.00, 0.89	<0.000
Southern box	7.81	7.63	0.00, 22.76	0.002
Northern box	0.39	0.41	0.00, 1.19	<0.000
<b>(e) Total demand (incorporating baleen whales and fish)</b>				
Whole box	2580.32	n/a	n/a	0.243
On-shelf	1117.63	n/a	n/a	0.276
Shelf break	468.07	n/a	n/a	0.226
Off-shelf	1027.28	n/a	n/a	0.226
Southern box	1368.30	n/a	n/a	0.257
Northern box	1019.75	n/a	n/a	0.192

The estimated standing stock of krill in the survey area at the time of survey of was 580000 ( $\pm 95\%$  CI: 0, 1100000) tonnes of krill (Jon Watkins Pers. Com.). Thus the daily consumption rates of krill by fur seals is 0.33% and for all species considered in this study it is 0.45%.

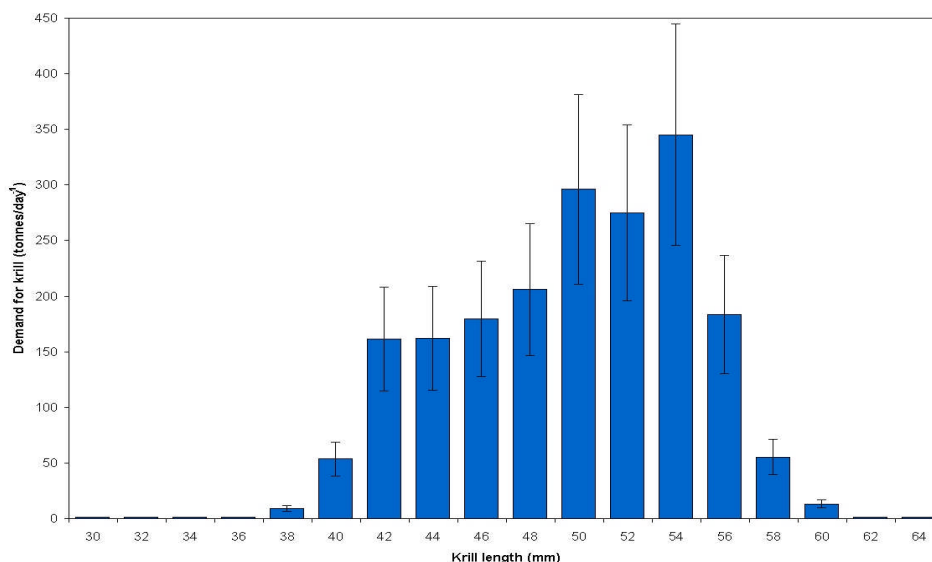
#### ***5.3.4 Spatially specific demand***

Demand was not equally distributed throughout the region, with the highest rates (for Antarctic fur seals only) being found in the on-shelf region, 0.202 tonnes km<sup>2</sup> day<sup>-1</sup>, and southern sector, 0.190 tonnes km<sup>2</sup> day<sup>-1</sup>. There was no difference between consumption rates between the shelf break and offshore region. This pattern was found for both Antarctic fur seal only demand and when all predators were considered, see Table 5.8.

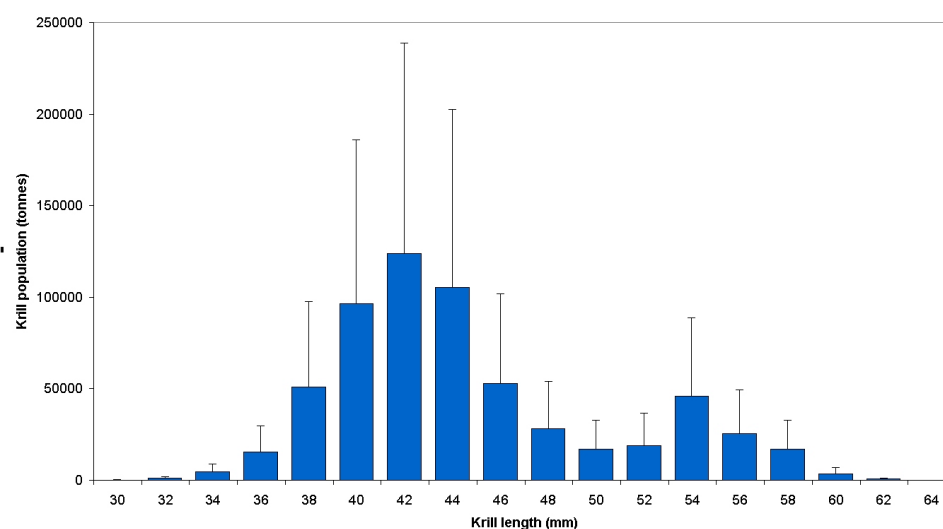
#### ***5.3.5 Length specific demand and consumption***

Division of total demand into specific krill length categories revealed the distribution of demand to be similar between all predator species. It was concentrated towards the upper end of the length frequency range derived from net caught krill, with demand peaking at 50 and 54mm (Figures 5.5, 5.6 and 5.7). This trend was consistent with previous years (Reid and Arnould 1995; Reid et al. 1996; Croxall et al. 1997).

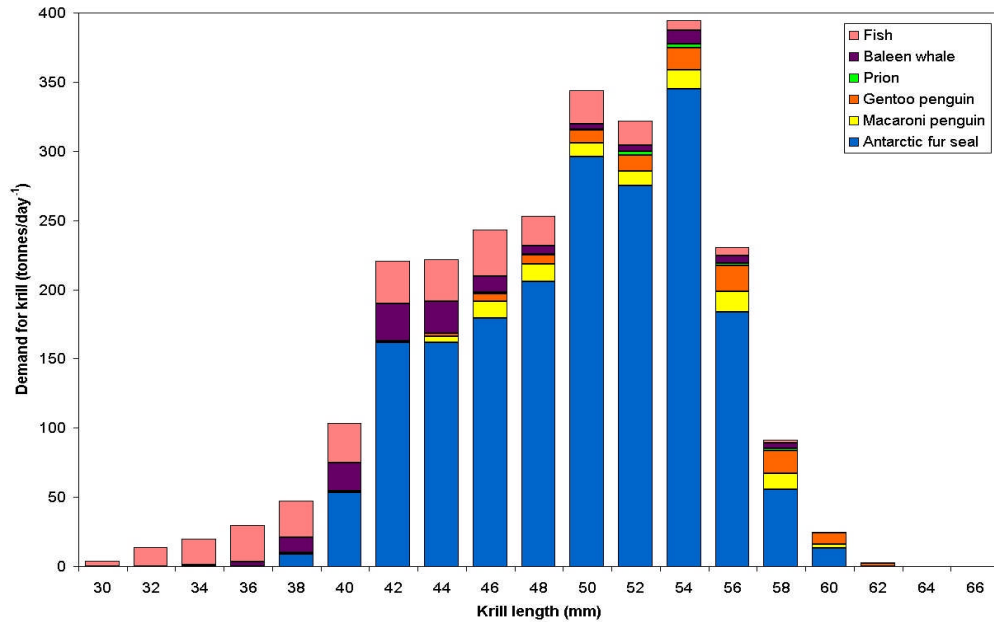
Consumption rates (the proportion of the krill stock eaten per day) were estimated within each krill length class (shown in table 5.9 and 5.10) the highest consumption rate was 1.81% for 50 mm krill over the whole box. When demand was broken down into sub regions, this consumption rate for 50 mm krill was 4.79% within the off-shelf region.



**Figure 5.4.** Mass adjusted length specific demand for krill (tonnes day<sup>-1</sup>) by Antarctic fur seals within the WCB during the period 13/01/2002 – 28/01/02. Error bars show 95% confidence, based on variance in seal demand, and do not incorporate uncertainty of diet length composition.



**Figure 5.5.** Mass adjusted length-frequency distribution of krill from net samples within the study area during the period 13/01/2002 – 28/01/02,  $n = 2934$ . Error bars show 95% confidence intervals are based on variance in population density, and do not incorporate uncertainty of length frequency within the population.



**Figure 5.6.** Mass adjusted length specific demand for krill (tonnes day<sup>-1</sup>) by Antarctic fur seals, macaroni penguins, gentoo penguins, prions, fish and baleen whales. For Antarctic fur seals, macaroni penguins and gentoo penguins length specific demand is specific to late January 2002. Prion demand is based on densities present during January 2002, with diet and energetic demand estimated from the literature. Estimates of demand for fish and baleen whales are estimated based on values in the literature; see methods for specific details.

### 5.3.6 Considering krill growth rates

The average growth rate in krill biomass within the WCB at the time of survey was 0.56% ( $\pm$  SD 0.6) of total mass per day. Growth rates were much higher for smaller krill, ranging from 1.15% for 38mm krill to 0.09% for 60mm krill.

Though the overall consumption rate is lower than the overall growth rate, this is not true for the longer krill length categories, for krill 48 mm and longer, demand exceeded growth rates, this is indicated in bold in Table 5.9 and Table 5.10.



**Table 5.9. Length specific (mm) biomass consumption by Antarctic fur seals and growth rates per day (% of total biomass day<sup>-1</sup>). Consumption rates are also presented by sub-regions of the WCB. Figures in bold indicate where consumption rates are greater than growth rates. All rates are specific to late January 2002.**

<b>Length</b>	<b>All WCB</b>	<b>On shelf</b>	<b>Shelf break</b>	<b>Off shelf</b>	<b>Southern</b>	<b>Northern</b>	<b>% Growth</b>
38	0.02	0.01	0.01	0.05	0.01	0.04	1.15
40	0.06	0.04	0.02	0.15	0.04	0.11	1.05
42	0.14	0.10	0.06	0.36	0.09	0.26	0.89
44	0.16	0.12	0.07	0.43	0.10	0.31	0.80
46	0.36	0.27	0.15	<b>0.94</b>	0.23	0.68	0.74
48	<b>0.77</b>	0.58	0.32	<b>2.04</b>	0.50	<b>1.48</b>	0.65
50	<b>1.81</b>	<b>1.35</b>	<b>0.75</b>	<b>4.79</b>	<b>1.18</b>	<b>3.47</b>	0.57
52	<b>1.51</b>	<b>1.13</b>	<b>0.63</b>	<b>4.00</b>	<b>0.98</b>	<b>2.89</b>	0.49
54	<b>0.79</b>	<b>0.59</b>	<b>0.33</b>	<b>2.08</b>	<b>0.51</b>	<b>1.50</b>	0.41
56	<b>0.75</b>	<b>0.56</b>	<b>0.31</b>	<b>1.98</b>	<b>0.49</b>	<b>1.44</b>	0.29
58	<b>0.34</b>	<b>0.25</b>	<b>0.14</b>	<b>0.90</b>	<b>0.22</b>	<b>0.65</b>	0.17
60	<b>0.39</b>	<b>0.29</b>	<b>0.16</b>	<b>1.03</b>	<b>0.25</b>	<b>0.75</b>	0.09
<b>All</b>	<b>0.33</b>	<b>0.25</b>	<b>0.14</b>	<b>0.88</b>	<b>0.22</b>	<b>0.64</b>	<b>0.56</b>

**Table 5.10. Length specific (mm) biomass consumption by all predators (see text) and growth rates per day (% of total biomass day<sup>-1</sup>). Consumption rates are also presented by sub-regions of the WCB. Figures in bold indicate where consumption rates are greater than growth rates. All rates are specific to late January 2002.**

<b>Length</b>	<b>All WCB</b>	<b>On shelf</b>	<b>Shelf break</b>	<b>Off shelf</b>	<b>Southern</b>	<b>Northern</b>	<b>% Growth</b>
38	0.10	0.07	0.04	0.25	0.06	0.21	1.15
40	0.11	0.08	0.05	0.29	0.07	0.23	1.05
42	0.19	0.14	0.08	0.49	0.12	0.37	0.89
44	0.22	0.16	0.09	0.56	0.14	0.43	0.80
46	0.47	0.36	0.21	<b>1.17</b>	0.31	<b>0.89</b>	0.74
48	<b>0.93</b>	<b>0.70</b>	0.41	<b>2.31</b>	0.61	<b>1.72</b>	0.65
50	<b>2.08</b>	<b>1.57</b>	<b>0.88</b>	<b>5.24</b>	<b>1.36</b>	<b>3.86</b>	0.57
52	<b>1.74</b>	<b>1.32</b>	<b>0.74</b>	<b>4.32</b>	<b>1.14</b>	<b>3.18</b>	0.49
54	<b>0.88</b>	<b>0.67</b>	<b>0.37</b>	<b>2.18</b>	<b>0.58</b>	<b>1.59</b>	0.41
56	<b>0.91</b>	<b>0.71</b>	<b>0.39</b>	<b>2.11</b>	<b>0.61</b>	<b>1.55</b>	0.29
58	<b>0.52</b>	<b>0.43</b>	<b>0.23</b>	<b>1.00</b>	<b>0.36</b>	<b>0.74</b>	0.17
60	<b>0.67</b>	<b>0.56</b>	<b>0.25</b>	<b>1.09</b>	<b>0.46</b>	<b>0.80</b>	0.09
<b>All</b>	<b>0.43</b>	<b>0.33</b>	<b>0.19</b>	<b>1.08</b>	<b>0.28</b>	<b>0.81</b>	<b>0.56</b>

### *5.3.7 Demand supply balance in previous years*

The density of krill in the year of this study (2002) was higher than many previous years. Comparison of the demand and growth rates estimated at the time of survey found consumption rates to be higher than growth in all but three of the eleven years considered. See Table 5.11.

**Table 5.11.** The balance of growth and consumption rates in previous years within the WCB study region. The consumption-growth rate balance was expressed as growth (*G*) minus consumption (*C*), a negative figure indicates that demand exceeded growth.

<b>Year</b>	<b>Krill in WCB (tonnes)</b>	<b>Consumption rate (<i>C</i>)</b>	<b><i>G-C</i></b>
1991	52360	3.71	-3.15
1992	791010	0.25	0.31
1993	547910	0.35	0.21
1994	61710	3.14	-2.58
1995	n/a	-	-
1996	222530	0.87	-0.31
1997	209440	0.93	-0.37
1998	177650	1.09	-0.53
1999	99110	1.96	-1.40
2000	102850	1.89	-1.33
2001	287980	0.67	-0.11
2002	580000	0.33	0.23

## 5.4 DISCUSSION

This study is different to other estimates of seal or seabird prey demand in a number of ways:

Many studies are based on estimates of predator demand averaged over longer time periods, an entire breeding season or even a whole year (Barrett et al. 2002; Hewitt et al. 2004c), and though many studies do incorporate seasonal changes (Boyd 2002a) this is only compared as an annual budget with prey availability, though see Gremillet et al. (2003). This study was specific to the end of January 2002. At this time of year, Antarctic fur seals at South Georgia, are providing food for rapidly growing offspring and are not only at their peak annual energy demands but are also at their most sensitive to low krill availability (Barlow et al. 2002; Boyd 2002a). Boyd (2002b) demonstrated the sensitivity of demand estimates to fine scale changes in demographic distribution and time of year.

Most previous studies have based the population component of demand models on scaling up a land based estimation of a total population (Croll and Tershy 1998; Boyd 2002a), or on line transect derived estimate of total population size averaged to a wide area (Joiris et al. 1996) i.e. they are often boundary unspecific. This study was based on line transect derived density estimates that are specific to a defined ( $10640 \text{ km}^2$ ) study area, the WCB. Within this study area densities are specific to sub-sections characterised by depth, a major underlying physical feature of the region.

Often, by averaging prey supply and demand over time, or over a large geographical area (Trathan et al. 1995), we may believe that supply comfortably meets demand, and in doing so may miss pressure points on the

system, where, within specific areas of high demand or low availability, demand may not be met by supply (Hewitt et al. 2004c; Cross et al. 2005). This study allows us to pinpoint demand within these regions at the most critical time of year. This understanding of localised supply and demand is essential if we are to understand important ecosystem processes, that could prove essential in mitigating the impacts of increasing pressure from fisheries (Nettleship et al. 1984; Duffy and Schneider 1994; Hewitt et al. 2004b).

#### ***5.4.1 Individual demand***

The flexibility of the individual demand model enabled the use of slightly different methods according to the most up-to-date and accurate data available for each species whilst retaining the same essential structure and consistent methods of error estimation. For macaroni penguins field metabolic rates were measured using implanted heart rate loggers (Butler et al. 2004; Green et al. 2004; Green et al. 2005b), concurrently with the at sea survey. This gives the most accurate demand requirements for macaroni penguins that could be currently derived. At the time of the study macaroni penguins were at the mid point of the transition between brood guard and the start of chick rearing. These values were higher than previous estimates of FMR for macaroni penguins which estimated FMR averaged between brood guard and crèche to be  $708 \text{ kJ kg day}^{-1}$  (Green et al. 2002). Upon moving into chick rearing, adult energy requirements increase significantly and this could account for the higher estimation of FMR for the empirical measurements during this study (Croxall 1984; Davis et al. 1989; Boyd 2002a). Metabolic rates of gentoo penguins, the highest being during brood guard ( $688 \text{ kJ kg day}^{-1}$ ), were lower than those for macaroni penguins but this has been the case in

previous estimates (Davis et al. 1989; Bevan et al. 2002). For Antarctic fur seals, gentoo penguins and prions, metabolic rates were taken from the literature based on previous studies of the same study populations at Bird Island at the same time of the season.

#### **5.4.2 Overall demand**

The total daily demand for krill by Antarctic fur seals, gentoo and macaroni penguins and prions together for the whole WCB was 2097 ( $\pm$  95% CI 417, 3772) tonnes day<sup>-1</sup>. Antarctic fur seals accounted for 93% of this demand; macaroni and gentoo penguins took 3.95% and 3.05% respectively, with prions taking just 0.48% of the total daily demand (Table 5.8). Adding whales and fish increased this demand to 2582 tonnes day<sup>-1</sup>, with fish making up 68% of the 421 tonne increase.

The estimated standing stock of krill in the survey area at the time of survey of was 580000 ( $\pm$ 95% CI: 0, 1100000) tonnes of krill. Thus the daily demand for krill by all the species considered in this study was 0.33% of the total stock. With the assumptions that all of this krill was available to predators, that there was no growth in the krill stock and that it is a closed stock, this stock would be consumed in 298 days by seals and 225 days by all predators combined.

The estimated demand by macaroni and gentoo penguins was much lower than that for the same area by recent estimates (146 vs. 5298 tonnes) (Hewitt et al. 2004c). The surveys of small penguins in this study did find lower estimates than previous studies, however, even with similar density estimates to previous studies, it would be difficult to explain all the difference in estimated demand.

### ***5.4.3 Krill growth rates and length specific demand***

When considered for the whole population we found krill growth rates to be increasing the population's biomass faster than it was depleted by predator demand. These values do not include krill mortality rates, but do suggest that the region may be able to support its predator biomass without a net influx of krill; this would have significant consequences for our understanding of South Georgia ecosystem. This krill surplus however, does not exist when we consider krill length. All predators considered by the study (excluding baleen whales) showed selective preference for longer krill, whose growth rates are much slower than shorter krill, and for all krill longer than 48 mm demand was found to be greater than supply by growth. Murphy & Reid, (2001) did find a tendency for the modal length of the krill population to reduce over the breeding season, but any shift away from the predators preferred krill-length frequency is presumably an increased stress at this critical time of year.

There is much more to krill population composition than krill length. Previous studies of predator diet composition in the region have found gravid female krill in the diet of Antarctic fur seals to be more prevalent than in concurrent net hauls (Reid et al. 1996). This is probably because gravid female krill are possibly less manoeuvrable or slower than shorter or male krill. A second reason may be that larger, sexually active female krill may represent a higher energy gain per catch. Thus smaller or male krill not only offer a smaller return per catch, but also that they maybe harder to catch in the first place. This would suggest that any decrease in the krill population's

modal length frequency would make profitable foraging harder for krill predators.

This finding suggests that there is indeed a real need for a net influx of larger krill into the ecosystem from elsewhere. Any krill stock entering the WCB must have already suffered some predation pressure, but the extent of this is unknown. It would be interesting to compare krill length frequencies up and downstream of South Georgia.

#### ***5.4.4 Spatially specific demand***

Fur seal females can concentrate food energy as milk, and have longer foraging trips than penguins who regurgitate whole prey to their young (Trathan et al. 1998b; Staniland and Boyd 2003). They are thus able to forage further from shore and bring energy back to their pups from resources beyond the range of penguins. Consequently, we may expect competition for prey to be higher near the colony than further from it (see Lewis et al. (2001)). The predator-prey balance differed within different regions of the WCB. As would be expected, the study found similar krill demand to be slightly higher on-shelf than off-shelf, though there was no difference between demand between the off-shelf and shelf-break regions. Krill density however was found to be higher over the shelf than off shelf, with the result that consumption rates in the off-shelf region exceeded growth rates. If this were a consistent pattern, it would mean that competition for krill may be higher in the off-shelf than the on-shelf region. This would have extensive consequences for our understanding of the South Georgia ecosystem, but it should be remembered that this is the result of a one-month survey, and may not represent more general patterns over longer time periods.



#### ***5.4.5 Supply demand balance in previous years***

During the season of this study there was no evidence that fur seals had difficulty finding sufficient food. However in previous years, low estimates of krill density within the region have coincided with higher than average breeding failure in krill dependent predators (Croxall et al. 1999; Barlow et al. 2002; Brierley et al. 2002; Reid 2002; Trathan et al. 2006). In only three out of the eleven years examined did krill growth exceed consumption, two of these years where consumption was much greater than krill growth (1991 and 1994), coincided with years where the reproductive output of krill predators was very much reduced.

#### ***5.4.6 Future work***

Demand models proved to be most influenced by population composition and population size rather than to behavioural or energetic parameters. Our weakest link in being able to draw conclusions from this study lies in improving estimates of predator and possibly more importantly, krill, densities (Demer and Conti 2005). Future work involving more surveys, possibly spread over the season and improved density estimates for both predator and prey are essential for understanding of this predator-prey balance, and in turn for the management of this crucial predator, krill rich region of commercial interest.

Whilst there are tremendous benefits in focusing intensively on one fine-scale area, it could be misleading to expand the findings of the study box to the rest of South Georgia. The WCB is situated in a high biomass, high demand region, and by nature this makes it more difficult to model and to

extrapolate from. It would therefore be interesting to investigate the krill/demand balance in other areas around South Georgia.

Murphy et al. (2004) illustrated that though there is a strong flux of water and krill through the region, this rate is very variable and it may be that for shorter periods of time the krill stock at South Georgia is less well replenished. Though the overall amount of krill reaching South Georgia in a season may be considerable it is important to understand how such a short-term reduction in flux may influence the reproductive output of predators. This same fine scale understanding of flux also needs to be viewed spatially, it may be that some critical areas may be replenished whilst others are not, understanding the local variability in the spatial demand supply balance, both from studies such as these, and by looking at changes in habitat use in times of increased pressure are essential.

Through the many factors investigated in this chapter, it is clear that the supply and demand balance for krill over one month of summer is extremely fine. There is no summer krill fishery at South Georgia and it seems prudent to keep it that way. Winter predator demand for krill is lower, as many macaroni penguins have left the system and female Antarctic fur seals are no longer foraging for their pups. However, many female Antarctic fur seals and potentially juveniles do still remain in the region. It is important to apply the procedures of estimating at-sea surveys of predator density and demand developed within this thesis to the South Georgia ecosystem in winter.



## CHAPTER SIX

### General discussion and conclusions

In the Scotia Sea there are numerous studies linking the success of predators, and the availability of krill to both regional and larger scale processes (Murphy 1995; Fedoulov et al. 1996; Fach et al. 2002; Jessopp et al. 2004; Forcada et al. 2005; Trathan et al. 2006). Moreover, Murphy et al. (2004) illustrates that even when the overall amount of krill reaching South Georgia in a season is average, there are still short term reductions or spatial variability in fluxes (i.e. there may be large differences in flux between areas at small-scales). In addition long term estimates of predator population size from Bird Island South Georgia showed that a number of species, though not fur seals, experienced a relatively rapid decline in the early 1990s related to changes in prey availability (Reid and Croxall 2001). At the same time studies of long term plankton records from the Scotia Sea have revealed major declines in krill abundance possibly associated with changes in sea ice extent (Atkinson et al. 2004).

Consequently, from both an academic and management perspective understanding the regional and local mechanisms that underlie krill variability and abundance at South Georgia, and how these interact with the ecology of predator populations is of prime importance. The purpose of this thesis has been to better understand the role that predators play in the krill flux model and in turn to understand the impact of krill variability on predators. As part of a long-term monitoring programme data have been collected over recent

decades at the Bird Island research station about the diet, energetics and behaviour of krill predators (Reid et al. 1997b; Croxall et al. 1999; Trathan and Croxall 2004; Green et al. 2005b). This thesis integrates some of these data with data from ship-based observation. Croll et al. (1998) demonstrated the advantages of integrating methodologies to better understand the role of top predators in the marine ecosystem.

This thesis integrates concurrent (and published) individual energetic, diet and behavioural studies with a multi-disciplinary cruise measuring predator and prey distribution at-sea to determine the abundance and distribution of krill predators and their demand for krill to the northwest of South Georgia. The thesis has three main sections (1) the number of predators (2) the distribution of predators and (3) the demand for krill by these predators.

### **6.1 The number of predators**

The estimation of abundance and its variance is dependent upon robust survey design; surveys of organisms that are spatially clumped, high in abundance and whose distribution is related to large-scale environmental features can be problematic. The survey design used in this study was a well established one, developed for estimating the density of Antarctic krill, an animal whose distribution is similarly abundant and patchy at a range of scales and whose distribution is related to the underlying bathymetry of the region (Veit et al. 1993; Trathan et al. 2003). This krill survey design also proved robust for estimating the density and variance of some krill predators, whose distribution is similar in nature to that of krill. This has advantages in

being able to derive confidence intervals for predator and prey concurrently from the same survey.

The main subject animal of this thesis was the Antarctic fur seal, and this was the first study attempting to quantify the abundance of Antarctic fur seals at-sea in the region, and is the second attempt at quantifying otarid seals in open water from a transect survey, see also Buckland et al. (1993b); in the course of doing so, analysis methods were developed. This was especially so with the added consideration of empirically derived dive behaviour.

Where dive durations are short (more the case with otarid than phocid seals) and the seals are numerous, our results indicate that useful estimates of seal density can be achieved. We estimated the density of seals in the Western Core Box (WCB) to be 39.64 seals  $\text{km}^{-2}$ , with the number of seals within the 10640  $\text{km}^2$  study area being 404000 (CV = 13%), an increase of 112% from the number of seals actually observed without adjustment for differences in observability.

Density estimates of other krill dependent species within the study area were also attempted. These were macaroni penguins (*Eudyptes chrysolophus*) 4.39 birds  $\text{km}^{-2}$  (CV = 21%), gentoo penguins (*Pygoscelis papua*) 4.64 birds  $\text{km}^{-2}$  (CV = 23%), and Antarctic prions (*Pachyptila desolata*) 27.01 birds  $\text{km}^{-2}$  (CV = 56%). There is little evidence in curves describing the decrease in detection probability from observer that penguins (Figure 3.1) were much harder to sight than Antarctic fur seals (Figure 2.7). However, penguins by nature of their size and colouring are difficult target to spot and even with all corrections applied, the fact that we estimated much lower densities than Hunt et al. (1992) in the same region and that we sighted

similar numbers of macaroni and gentoo penguins do raise questions about estimated penguin densities, in this study it was not possible to estimate perception bias and this should be considered in future studies. Despite a reduced estimate of macaroni penguins population size (Trathan 2004) there are many more macaroni than gentoo penguins at South Georgia (Croxall and Rothery 1995; Trathan et al. 1996b).

## **6.2 The distribution of predators**

*Is the distribution of lactating Antarctic fur seals state or prey-resource dependent?*

The overall population of Antarctic fur seals around South Georgia is thought to comprise of male, female, breeders, non-breeding adults and juveniles. Boyd et al. (2002a) estimated juvenile Antarctic fur seals to account for 62% of total Antarctic fur seal demand yet, most of our understanding about Antarctic fur seal distribution comes from telemetry studies of lactating Antarctic fur seals foraging from Bird Island (Boyd et al. 1991; Boyd et al. 1994; Boyd 1996; Boyd et al. 1998; Boyd 1999; Boyd et al. 2001; Boyd et al. 2002; Staniland and Boyd 2003). These lactating female seals are central place foragers; constrained in their choice of foraging location by having to return regularly to land to feed their pups. It was thus unclear whether animals without the same life-history constraints (juveniles, non-breeders or males) would show the same preferences in foraging locations. That is, does the need to regularly return to land influence choices in foraging location (where foraging would be state dependent)? Or are central place foraging seals still

able to exploit the same optimal foraging environments of less-constrained animals (where foraging is considered to be prey-resource dependent)?

By comparing at-sea distributions and habitat preferences from individual based techniques (satellite telemetry of lactating females) and from surveys of the whole population (line transect surveys within the same region) it was possible to determine whether the distribution and habitat preferences derived for lactating females foraging from Bird Island was representative of the at-sea fur population as a whole.

Where direct comparisons at different spatial scales were made between transect and telemetry derived distributions no conclusive relationships were found. The distribution estimated from telemetry is averaged over the survey period. The distribution derived from transects, however, is only a snapshot of the distribution at the time of the survey. The highly heterogeneous nature of marine ecosystem means that though underlying patterns may be present, we may not find them with these snapshot samples. A better way to investigate these similarities is by looking at the underlying factors relating to their distribution. General Additive Models (GAM) models based on the relationship between seal density (derived from transect and telemetry) and the physical environment were therefore developed. These found the same factors influencing seal distribution in both models, and there was no difference in the patterns in seal distribution between the two models.

Seal density was found to decrease with distance away from the island, and increase in regions of high bathymetric slope, i.e. the shelf break region. These relationships with physical environmental parameters were



similar to those found by previous studies of the distribution of krill (Trathan et al. 2003). Whatever physical or biological cues drive seal distribution, at some scale their distribution must be related to that of their prey, krill. This study found the density of seals to be positively correlated to the concurrent distribution of krill along transects, at a wide range of scales.

The consideration of longer term patterns in ecology is essential (Thompson and Ollason 2001) and the similarities between the distributions derived by telemetry and transects means that we can use our extensive records of seal distribution derived by telemetry over many years to represent the population's at-sea distribution as a whole.

### **6.3 Predator krill demand**

As a function of their numerical dominance, this section of my thesis focussed primarily on the demand for krill by Antarctic fur seals, but also included estimates of krill taken by the other predators considered earlier in the study, prions and macaroni and gentoo penguins, as well as literature derived estimates of demand for whales and fish (Hewitt et al. 2004c). The study used metabolic rates and behavioural budgets from the literature and simultaneous sampling of diet composition for the same study population at the same time of season. The study differed from previous studies as it was based around the population of a study box, allowing fine-scale, spatially explicit demands to be calculated. Other estimates of predator demand have been based upon scaling the requirements of the estimated breeding population of krill predators. This combination of estimated individual energy demands and predator densities has enabled the first spatially specific demand estimate for krill by predators within the region to be calculated.

Antarctic fur seals within the WCB were estimated to require 1940 tonnes krill day<sup>-1</sup>. This demand was 0.33% per day of the WCB standing krill stock (from here on termed daily consumption rate). For Antarctic fur seals, gentoo and macaroni penguins, prions, whales and fish combined, the total demand estimate was 2580 tonnes krill day<sup>-1</sup>, a daily consumption rate of 0.45%.

The distribution of demand was not equally distributed through the study area, as would be expected, demand for krill was found to be higher in the on-shelf rather than off-shelf region. The supply and demand balance, however, was not equally distributed throughout the region, and greater daily consumption rates were found in the waters off-shelf (defined as waters deeper than 2000 m) than on-shelf (waters shallower than 500 m) (1.08% off-shelf compared to 0.33% on-shelf). This was due to lower krill availability off-shelf than on. This pattern is possibly specific to the time of survey, not necessarily the longer-term pattern.

It was clear from sensitivity analysis that the variable with the most influence over variability in the final demand estimates was the estimation of predator population size, this variable accounted for 79% of total variance. The greatest limitations of the model however are in prey availability and further effort into quantifying the krill supply demand balance should focus primarily on improving estimates of predator and prey densities.

It is essential to understand the spatial scales at which predators and prey interact (Rose and Leggett 1990; Harwood 2001). Reid et al. (2005) found that abundances of krill predators, including Antarctic fur seals were highest at 60 – 120 km from land and decreased sharply at distances beyond

150 km. This creates a overlap with krill fisheries, which almost entirely operate within 100 km of land (Reid et al. 2004). This study operated on a finer scale, concentrating on the distribution of predators up to 100 km from land. It has been assumed that at South Georgia the greatest competition for krill exists in the on-shelf region, yet, if the results of this study are correct, it would mean that central place foraging animals are not under a competitive disadvantage by being unable to travel beyond a region of potentially higher competition. Further, it would suggest that there are physical factors or krill behavioural traits that make areas further from the colony more profitable than those closer, over shelf areas.

When estimated for the whole WCB, for all lengths of krill, krill growth rates (0.56% of total mass per day) were found to be greater than the demand for krill by predators, however this was not the case when length specific demands were considered. For the larger sizes of krill (preferred by most predators), demand outstripped growth for all krill longer than 48 mm. It should be noted that even in years where there is no evidence of prey availability related breeding failure, a constant krill length-frequency is not maintained over the breeding season (Murphy and Reid 2001).

This study has taken a further step in understanding the nature of the predator-prey balance at South Georgia. It has found that though a net influx of krill may not be required to sustain demand (though it may well be in previous years), when length specific demand is considered there is a need for krill of greater size than would be found in an already highly predated krill stock. Quantification of the predator demands on krill, realised by this thesis, place an important piece of information into the krill flux equation, and

improve knowledge of how representative telemetry studies are of the population of Antarctic fur seals.



**CHAPTER SEVEN****Cited literature**

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## APPENDIX ONE

### The foraging distribution model of Boyd et al. (2002)

The model used tracks of central place foraging (Orians and Pearson 1979) female Antarctic fur seals, and their dive behaviour, recorded from two locations on South Georgia, Bird Island and Stromness (a bay to the southeast of Bird Island along the north coast of South Georgia). The model described the shape of a typical foraging event from a central point, the site of the offspring.  $M$  was used as a random variable describing the location of a foraging event, described as the location of a dive during the foraging trip. This gave a Probability Density Function (PDF)  $f_M(m|i)$  for the location of a foraging event during a foraging trip where  $M = m$  for any realization. Thus where there were  $N$  individuals in the population (as described in Boyd et al. (1993)) occupying site  $i$  the absolute density of foraging events was  $N_i[f_M(m|i)] p_s$ , where  $p_s$  is the probability that an individual is at sea as opposed to being ashore feeding its pup.

$M$  was described by two random variables:  $L$ , the distance of  $M$  from  $i$ , and  $\theta$ , the bearing from  $i$  relative to an imaginary line running parallel to the coastline. These in turn had PDFs described as  $f_L(l|i)$  and  $f_\theta(\theta^*|i)$ . Thus, the position coordinates  $(x_i, y_i)$  of  $M$  were defined by the functions  $g_i(x,y|l)$  and  $g_i(x,y|\theta^*)$ , assuming that  $l$  and  $\theta^*$  vary independently. The generalized PDF at  $(x,y)$  can be defined as follows:



$$f_i(x, y|i) = \begin{cases} \int_0^{\infty} g_i(x, y|l) f_L(l|i) dl \\ \int_0^{180} g_i(x, y|\theta^*) f_{\theta}(\theta^*|i) d\theta \end{cases}$$

They used no *a priori* decision criteria for defining either  $f_L(l|i)$  or  $f_{\theta}(\theta^*|i)$ . They used the empirical estimates of  $f_i(x, y|i)$  from satellite and TDR records deployed from Bird Island and Stromness to develop empirical distributions of  $f_L(l|i)$  and  $f_{\theta}(\theta^*|i)$ . These were generalized by fitting a gamma function to each distribution by least squares. The parameters  $c$  and  $b$  defined the shape and scaling respectively of the gamma functions (Evans et al. 1993). Since two sites were used to generate these distributions it was possible to test how well this function described foraging distribution by applying function derived from seals at Bird Island and Stromness and vice versa.

Thus the population distribution was given by:

$$f(x, y) = \sum_{i=1}^n f_i(x, y|i) N_i$$

Where there are  $n$  colonies or locations from which these seals forage.