

**Response to Change in the Environment:  
Population dynamics of Weddell seals in East Antarctica**

Samantha Elizabeth Lake

B..Sc. (Hons) Zoology Department, University of Tasmania

M. Sc. Zoology Department, University of Tasmania

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Re-sighting flipper tags of an adult female Weddell seal whilst she was breeding in a colony amongst the icebergs at the Vestfold Hills.

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## ABSTRACT

In this thesis, two inter-related hypotheses were explored: The first hypothesis was that Weddell seals forage over small spatial scales (10s to 100s of kilometers) and therefore experience, rather than move to avoid, resource limitation. The second hypothesis was a consequence of the seals experiencing periods of resource limitation *i.e.* that changes over time in resource availability affect the seals' annual rates of survival and reproduction so that these parameters can be used as indicators of foraging conditions.

Diet study supported the premise that Weddell seals forage over relatively small spatial scales. Prey types were characteristic of the continental shelf. Many prey types were from inshore habitats. There was regional, temporal and fine-scale variation in the diet indicating that seals were foraging nearby where scats were collected. However, the wide variety in potential prey types may minimize coupling between Weddell seal population dynamics and the abundance of any particular prey species.

Ground studies and satellite tracking from mid-winter showed that Weddell seals rest in areas of fast ice. There was indirect evidence for seals foraging further offshore in that many haul-out sites were adjacent to a lead of open water within which the seals could have traveled through the dense sea ice zone. The three tracked seals did rest regularly on coastal fast ice, suggesting that they were foraging within a limited area. Limited movement may be a behavioural strategy to navigate by spatial memory in the dark of Antarctic winter. Furthermore, evidence suggests that local seals communally use and maintain breathing holes in static ice, which may make access to and from the water reliable, despite temperatures well below freezing.

Multi-strata models showed that the proportion of females in breeding state did change over time. Breeding proportion averaged 0.70 per annum, and ranged from 0.53 to 0.88 per annum. This contrasts with the relatively small magnitude of temporal variability in probability of parous females surviving from year to year, and is qualitatively similar to temporal variation in probability of pups surviving first year of life. The magnitude of inter-annual variability in both the probability of producing a pup, and the probability of that pup surviving, demonstrates how tenuous each reproductive event is for this long-lived mammal species.

Better understanding of the teleconnections between El Niño - southern oscillation (ENSO) and local physical and biological processes might elucidate the loose connections sometimes observed between ENSO and Weddell seal reproduction. At this stage, it is simply noted that the longest El Niño (warm) event in the record of 113 years (1990-1995), closely followed by another very severe El Niño

event (1997), did coincide with low reproductive rates of Weddell seals at the Vestfold Hills throughout the last decade of monitoring. In general, evidence suggests that the purported trend for increasing frequency and intensity of El Niño events could be detrimental to Weddell seals and the inter-dependent aspects of Antarctic ecosystems.

## STATEMENT OF PUBLICATION AND CO-AUTHORSHIP

The following publications were produced as part of this thesis:

Lake, S. E., H. R. Burton and J. van den Hoff (2003). Regional, temporal and fine-scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica. *Marine Ecology Progress Series* 254: 293-305.

Lake, S., S. Wotherspoon and H. Burton (2005). Spatial utilisation of fast ice by Weddell seals *Leptonychotes weddelli* during winter. *Ecography* 28: 295-306.

Lake, S., H. Burton and S. Wotherspoon (2006). Movements of Weddell seals during the winter months. *Polar Biology* 29: 270-279.

Heil, P., C. W. Fowler and S. E. Lake (2006). Antarctic sea-ice velocity as derived from SSM/I imagery. *Annals of Glaciology* 44: 361-366.

Lake, S., H. Burton, R. Barker and M. Hindell (submitted). Annual Reproductive rate of Weddell seals in Prydz Bay, east Antarctica, 1973-2000. *Marine Ecology Progress Series*

As well as my supervisors, these people and institutions contributed to the work undertaken as part of this thesis (in alphabetical order):

Richard Barker (Otago University) provided advice for modeling of mark and re-sight data

Simon Wotherspoon (University of Tasmania) ran the statistical analysis of diet data, distribution data and some aspects of satellite tracking data.

Detailed signed statements concerning the proportion of work undertaken for each of the publications listed above are held with IASOS.



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# Chapter 1

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## Introduction

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### *Antarctica and climate change*

Recent reports leave little doubt of the significance of changes now taking place to world climate (Intergovernmental Panel on Climate Change 2001). Polar regions are highly sensitive to both natural and human-induced change, due to feedback mechanisms between cryosphere (frozen water systems), atmosphere and ocean (Watkins and Simmonds 2000, Liu et al. 2004, Simmonds and King 2004). Antarctica offers international scientists the opportunity to investigate the consequences of climate change as a shared priority in a natural laboratory with few other anthropogenic effects (Howard-Williams 2001). However, there are problems comprehending variability in the Southern Ocean, mainly due to paucity of observations (Constable et al. 2003). Continuous or regular observations over long time intervals (years and decades) are required to characterize variability at inter-annual and inter-decadal time-scales. Ships cannot provide long-term monitoring, certainly not in sea ice. Specific ocean surface phenomena (e.g. sea ice cover) can be measured by satellite sensors, whilst additional parameters can be measured insitu. New technology has enabled major advances in the scientific understanding of oceanic processes (National Research Council 1994). Still, there are problems with continuity of coverage between satellites, harsh environmental conditions, and power sources for instruments, limiting time series.

Similarly, there are practical difficulties monitoring the biota of the Southern Ocean. It is for this reason that observations of land-based marine predators are so valuable. Studies of these species are among the few time series that provide signals of variation, potentially in lower trophic levels. Seals and sea birds forage at sea whilst reproducing on land or ice. Some populations reproduce in areas near Antarctic stations, where regular observations have been logistically feasible. In the Antarctic and sub Antarctic, this includes Weddell seals (*Leptonychotes weddellii*) in Prydz Bay; Adelie penguins (*Pygoscelis adeliae*) and Weddell seals in the Ross Sea; southern fulmars (*Fulmarus glacialisoides*), snow petrels (*Pagodroma nivea*) and emperor penguins (*Aptenodytes forsteri*) at Terre Adélie; and southern elephant seals (*Mirounga leonina*) and leopard seals (*Hydrurga leptonyx*) at Macquarie Island (ACE CRC Workshop 2005). In monitoring these isolated populations, it is assumed that elements of their behaviour, reproductive output and health are signs of availability and quality of food (Hindell et al. 2003). For air-breathing predators, sea ice structure is also likely to influence foraging success.

### *Monitoring studies*

Population parameters such as reproductive output, survival and abundance are, in themselves, quantitative indicators of the status of marine predators. As part of a suite of parameters from various populations, they provide a 'snap-shot' of the status of the Antarctic environment. However,

interpreting variation in these parameters with regard to the environment is the ultimate value that can be added to marine predator time-series (Constable et al. 2003).

Ascertaining links between predator 'performance' and marine ecosystems is particularly challenging in Antarctica where there is minimal theory for meso and local scale physical phenomena, even less regarding the consequences for primary, secondary, and tertiary production (Constable et al. 2003). Exacerbating difficulties, there is unlikely to be a linear relationship between prey abundance and predator performance, since predators may compensate for declining abundance by increasing foraging effort or switching to other prey types (Hindell et al. 2003). Furthermore, when sense is made of predator response, that 'response' can only be correlated with environmental events and thereby generate hypotheses of causal mechanisms. It is rare that causal links can be demonstrated.

Nevertheless, there are many examples where population dynamics of Antarctic land-based marine predators are in accord with large scale physical phenomena (Whitehead et al. 1990, Testa et al. 1991, Lunn et al. 1994, Boyd et al. 1995, Reid and Croxall 2001, Croxall et al. 2002, Fraser and Hofmann 2003, Jenouvrier et al. 2003, Weimerskirch et al. 2003, Beuplet et al. 2005, Forcada et al. 2005, Jenouvrier et al. 2005, Lea et al. 2006). Antarctica is similar to other marine environments in that signals of reduced productivity commonly coincide with El Niño events (e.g. Trillmich and Limberger 1985, Le Boeuf and Reiter 1991, Trillmich and Ono 1991): One of the first studies to propose a link between El Niño – southern oscillation (ENSO) and the Southern Ocean was Testa et al. (1991), who reported time series data from Weddell seals. A decade later, scientists have documented ENSO forcing physical parameters in the Southern Ocean (Kwok and Comiso 2002, Yuan 2004). This type of inference, later confirmed by scientific fact, led Chavez et al. (2003) to conclude that physical regime shifts may even best be determined by monitoring marine organisms.

### *Weddell seal monitoring*

Testa et al. (1991) examined time-series data from several species of Antarctic seal, and found that Weddell seal reproductive rate was the closest correlate with ENSO. Reproductive rate was estimated using mark and re-sight data from McMurdo Sound. There have been two mark and re-sight programs of Weddell seals on the Antarctic continent – one at the Vestfold Hills and the other at McMurdo Sound. These programs are among the longest running studies of Antarctic predators.

Like most Antarctic species that are land-based, Weddell seals do not have a strong escape response and so are tractable to study, especially when with pup. They are large mammals (c.a. 200-350 kg) that rest on the surface of the fast-ice with eyes closed much of time, possibly because glare on the ice is

much brighter than in their underwater habitat. The breeding season is from October to December, when fast-ice provides stable substrate for vehicle surveys. Antarctic climate can be relatively benign at that time of year, facilitating the use of helicopters to locate seals in outer areas of fast-ice. Weddell seals are conspicuously dark on white ice substrate, making it easy to locate animals. Even untrained personnel can re-sight tagged individuals. These simple logistics make it possible to maintain Weddell seal mark and re-sight programs over time.

Weddell seals have a very different foraging niche to other Antarctic predators. They are the only predator to habitually use holes in continuous ice to breathe and haul out on the ice surface. Combined with dives to depths of 700 to 800 m (Testa 1994), Weddell seals are the only air-breathing predator capable of foraging in both benthic and pelagic habitats and throughout the seasonally ice covered oceans of the Antarctic continental shelf and slope. In so saying, Weddell seal foraging has not yet been fully characterised.

### *Weddell seal response to the environment*

It has already been established that Weddell seals are long-lived (Cameron and Siniff 2004) and that the proportion of females reproducing each breeding season varies over time, most likely in response to body condition and ultimately determined by foraging success (Siniff et al. 1977, Croxall and Hiby 1983, Testa 1987, Testa et al. 1990, Testa et al. 1991, Hastings et al. 1999). Other Antarctic predators have similar life-histories. Southern fulmars, Adelie penguins and Antarctic fur seals (*Arctocephalus gazella*) are also long lived with time-varying reproductive success (Whitehead et al. 1990, Lunn and Boyd 1993, Jenourvier et al. 2003, Forcada et al. 2005, Jenourvier et al. 2005). Commonly referred to as bet hedging (Stearns 1992), this life-history strategy generally corresponds with highly variable environments (Ferguson and Lariviere 2002).

Physical conditions in the Southern Ocean are highly variable, with cyclic changes in sea-ice extent, sea-surface-temperature, and sea-surface pressure. These natural cycles have been linked to ENSO and other principal modes of climate variability (Watkins and Simmonds 2000, Simmonds and King 2004, Turner 2004, Appendix 2). ENSO is dominant globally on decadal and sub-decadal scales, most readily apparent as a profound effect on weather and oceanic conditions across the tropical Pacific (Turner 2004). The link between ENSO and the Southern Ocean is via Rossby waves of atmospheric pressure in the Pacific, resulting in the Antarctic dipole - an out-of-phase relationship between South Pacific (Ross and Bellingshusen Seas) and South Atlantic (the Weddell Sea), either side of the Antarctic Peninsula (Yuan 2004). In turn, the Antarctic dipole is an integral component of the Antarctic Circumpolar Wave (ACW) (White and Peterson 1996). The ACW is a phenomenon

whereby anomalies in the physical environment change in phase as they effectively ‘propagate’ around the Southern Ocean, as part of the Antarctic Circumpolar Current and maintained by air sea interactions (Cai and Baines 2001). The ACW gives rise to at least some of the temporal and spatial variation in the Southern Ocean (Liu et al. 2004, Simmonds and King 2004).

Presumably long-lived species in the Southern Ocean have life-history strategies that maximize reproductive success over ENSO time scales. However, the frequency and intensity of ENSO fluctuations is changing, with more warm (El Niño) events and fewer cold (La Nina) events since the 1970s. The prolonged 1990-1995 El Niño event was unprecedented in the climate record of 113 years (Trenberth and Hoar 1996, Watkins and Simmonds 2000, Liu et al. 2004). This change in phase of ENSO could potentially be detrimental to Weddell seals. Mark and re-sight techniques are a basic tool for quantitative studies describing the effects of such change on the status of a species and, in combination with other monitoring programs, there is potential to reveal the proximate effects of ENSO in Antarctic ecosystems.

### *Thesis structure*

In this thesis, two premises were explored. The first premise was that Weddell seals forage over relatively small areas (10s to 100s of kilometers) and thus experience fluctuations in environmental conditions as opposed to moving to avoid resource limitation. The second premise was a consequence of the first i.e. that annual rates of survival and reproduction fluctuate over time in response to the local environment, and therefore can be used as evidence of change in the status of this species and corresponding aspects of Antarctic ecosystems.

Each chapter represents a discrete article. Overlap has been retained so that each chapter ‘stands alone’ as a scientific paper. Chapters 2-4 describe aspects of foraging ecology and have already been published. Chapter 5 is a multi-strata model of the annual rates of reproduction and survival of parous female Weddell seals, based on mark and re-sight data. Findings are assessed with regard to premises in Chapter 6, which is a synthesis of conclusions from previous chapters.

Co-authors are listed with the title and journal reference at the beginning of each chapter and in the statement of publication and co-authorship. During my period of candidature, I have co-authored another publication (Heil et al. 2006, Appendix 1). That work was undertaken initially to parameterise aspects of environment that influence the foraging success of Weddell seals.

### *Summary of data chapters*

Chapter 2 is a description of Weddell seal diet at various temporal and spatial scales. In the past, the breadth of diet of many pinniped species has limited power to detect differences except when profound changes occur (Hindell et al. 2003). I used both parametric and non-parametric multivariate statistics, and standardized for seasonal and/or spatial variation to assess regional, seasonal and inter-annual variation in diet.

Chapter 3 investigates the distribution of Weddell seals during winter by developing a resource selection function for the location of haul-out sites in fast ice at the Vestfold Hills. Generalized additive models were used to parameterize the distribution. The two strongest predictors of seal distribution were modeled using smoothed functions, rather than linear or log relationships, demonstrating how generalized additive models provided better fitting models, thus better predictions and more information for interpreting relationships than could be obtained by generalised linear models.

Chapter 4 is a report of satellite tracking for three adult females over six months from midwinter. The datasets were interpreted with regard to foraging range. Specifically, evidence was assessed with regard to foraging beneath fast ice as opposed to foraging offshore beneath dynamic ice whilst returning to fast ice to rest. Location data was obtained only when seals were resting on top of the ice, and all locations were in the area of fast ice that was associated with the Vestfold Hills. Thus results were tailored to show the pattern of use of discrete holes in the ice.

Chapter 5 quantifies annual reproductive rate and survival of parous (sexually mature) females using a multi-strata model of mark and re-sight encounter histories. This method of modeling annual reproductive rate is new and scientifically rigorous. Results indicate that annual reproductive rate is a temporally precise indicator of maternal condition, specific to each year of survey, and presumably reflects this predator's perspective of the state of the environment.

# Chapter 2

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## **Regional, temporal and fine-scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica**

Chapter 2 appears to be the equivalent of a post-print version of an article published as: Lake SE, Burton HR, van den Hoff, J. (2003) Regional, temporal and fine-scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica. *Marine Ecology Progress Series* 254:293- 305

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### INTRODUCTION

Diet studies of seals and seabirds are essential for understanding their role in marine ecosystems. These high-level predators can integrate information about several layers of primary and secondary production and thus can be used for describing and monitoring spatial and temporal ecosystem dynamics. Weddell seals are one of few high-level predators that forage in Antarctic coastal ecosystems. Their unique behavioural capacity to use networks of breathing holes allows them to live beneath continuous sea ice. Combined with the ability to dive to depths of 700 to 800 m (Castellini et al. 1994, Testa 1994), Weddell seals are the only air-breathing predator capable of foraging in both benthic and pelagic habitats throughout the ice-covered oceans over the Antarctic continental shelf.

The diet of Weddell seals has been described at several locations around Antarctica (Figure 2-1a), and repeated descriptions for specific locations have been relatively consistent. Two studies at the Vestfold Hills have revealed that both benthic and pelagic fish, and prawns, comprise the diet at the Vestfold Hills (Green and Burton 1987, Green et al. 1995). Pelagic fish are predominant in the diet at McMurdo Sound (Testa et al. 1985, Burns et al. 1998). Cephalopods are the main prey type at both South Shetland Islands and Mawson (Lipinski and Woyciechowski 1981, Clarke and McLeod 1982, Green and Burton 1987, Casaux et al. 1997). Other species of benthic and pelagic fish are consumed over the continental slope in the Weddell Sea (Plötz 1986, Plötz et al. 2001). This marked, regional variation in diet composition, and the huge area of ocean surrounding even coastal Antarctica, necessitates diet analysis at other locations to strengthen our understanding of Weddell seal foraging.

Antarctic waters have marked seasonal fluctuations in light and productivity, both factors being linked and attenuated by summer melt of snow and ice (Eastman 1993). In addition, climate and oceanography around the Southern Ocean cycle in 4 to 5 yr periodicity (White and Peterson 1996). However, seasonal and inter-annual variation has not yet been characterized for Weddell seal diet. The variation in diet described by Plötz et al. (2001) could have had both seasonal and inter-annual elements because seasons were sampled in different years and only one season was replicated. Variation in diet described by Green & Burton (1987) over 13 months and in 2 areas did not characterize seasonal changes because seasons were not sampled repeatedly and the scale of spatial variation was not considered. Green et al. (1995) compared scats (faecal samples) from several years collected over similar dates but from unspecified locations, and thus even that comparison of years could have been confounded by fine-scale spatial variation in diet composition.

This study evaluates fine-scale spatial and seasonal variation in Weddell seal diet, using scats collected in spring and summer for four years at the Vestfold Hills, and winter and spring for two years at Mawson. Diets were described for another two locations in summer, and regional comparisons were

standardised by time of year. Most of the collections were replicated, although not necessarily from the same sites and seasons in each year and at every location. The scats were collected from the top of sea ice. Research on Antarctic sea ice can be difficult in all seasons due to the changing extent of ice cover and remoteness. This analysis of 905 scats from 4 locations in east Antarctica almost doubles the description of the Weddell seal diet to date.

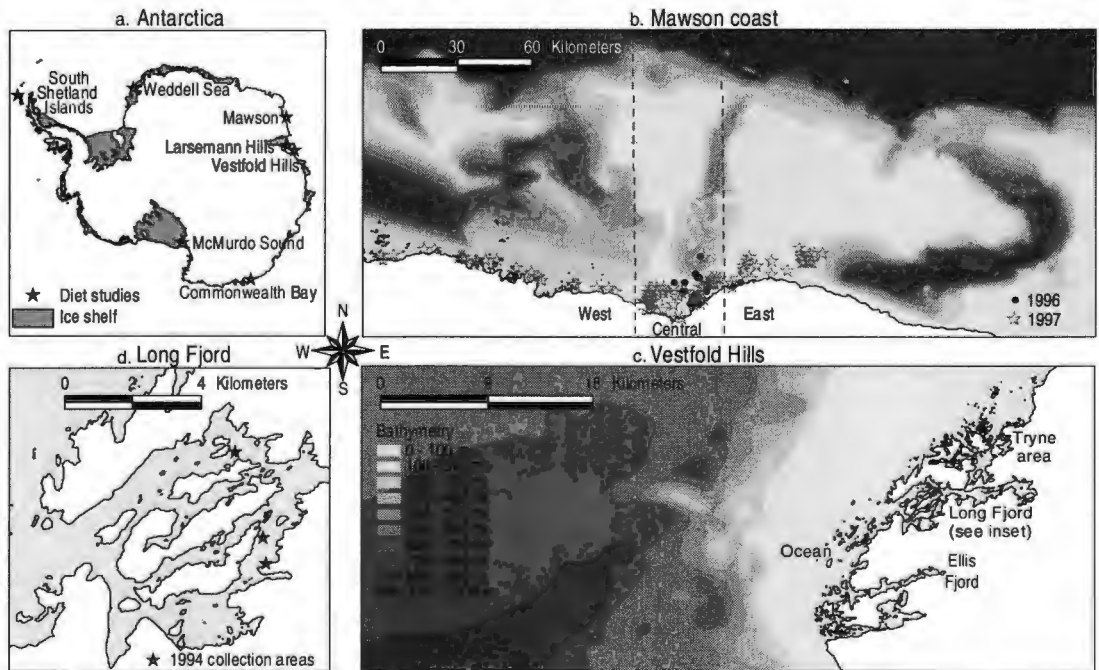


Figure 2-1 Locations of current and previous diet studies (a), specifying sample sites along the Mawson coast ( $68^{\circ} 00' S$ ,  $63^{\circ} 00' E$ ) (b), at the Vestfold Hills ( $68^{\circ} 33' S$ ,  $78^{\circ} 15' E$ ) (c), and fine-scaling sampling within Long fjord at the Vestfold Hills (d). Scale of bathymetry for the Vestfold Hills also applies to the Mawson coast.

## MATERIALS AND METHODS

Some species of seal eliminate prey hard parts by both defaecation and regurgitation (Pierce and Boyle 1991). However, whilst collecting over 900 scats, only 2 regurgitates were sighted. These contained undigested fish, squid and prawns apparently eliminated unselectively and possibly in response to over-consumption. Given these observations, it was assumed that Weddell seals generally eliminate all prey remains by defaecation and this study was based solely on faeces (scats). Only whole and relatively fresh scats were collected. Ice was not removed to measure the mass of scat. As in other

studies (e.g. Green & Burton 1987, Burns et al. 1998), a single scat of variable mass was the sampling unit. Samples were frozen until analysis.

### *New method for processing faecal samples.*

A new method of washing scats in a conventional clothes washer was developed based on a reference in Pierce & Boyle (1991), where terrestrial scats were washed in a machine encased in nylon stockings. The method was developed after finding that the open system elutriator of Bigg and Olesiuk (1990) was not suitable for Weddell seal scats because the already established method relied on a difference in the density of diagnostic remains compared to flocculent material. This difference could not be used in this study because the crustacean exoskeletons would have been washed away.

Bags of 2 sizes were constructed from scientific-grade plankton net. The smaller bag had a mesh diameter of 1 mm and the larger bag 0.25 mm. The bags were closed by Velcro™ and U-shaped so that they could be inverted and cleaned. Each scat was washed while nested in both bags. It took about 10 minutes for the flocculent material to be removed. It was possible using this technique to wash several scats separately but at the same time. Gentle agitation in water removed the flocculent without damaging even the most delicate remains, such as crustacean exoskeletons. The scats were washed outside the laboratory and the faecal odour was greatly reduced by the time the remaining hard parts were brought inside for sorting. The bags for each scat were washed in a 20 l bowl, the contents of the bowl drained through a 0.25 mm mesh sieve, and the contents of the sieve transferred to a sorting dish. Retention capabilities of this system were tested by seeding the bags with 1 mm, 0.7 mm, and 300 µm glass beads, and processing scats as usual. Approximately 95% of the medium and large-size beads were retrieved from the first wash. This indicated that prey remains greater than 0.7 mm were being recovered, and that there was minimal carry-over of remains within the mesh bags. As a second check, a 100 µm mesh sieve was placed at the outfall and its contents confirmed that all sagittal otoliths, cephalopod beaks and whole crustacean exoskeletons had been retained in the bags.

### *Identification and quantification of prey*

Fish taxa were identified and quantified by sagittal otoliths with reference to Williams and McEldowney (1990). The number of fish per scat was quantified as the maximum number of either left or right otoliths for each species. Lengths of uneroded otoliths were measured by digital image analysis using a microscope and image analysis software. Standard length and body mass (BM) of fish

were estimated from otolith lengths using species-specific allometric equations from Williams & McEldowney (1990). *Trematomus* type otoliths (Williams & McEldowney 1990) were distinct from *Pleuragramma antarcticum* otoliths, which were distinct from channichthyid otoliths. *Trematomus* type otoliths too eroded to identify were categorised as eroded benthic fish, except for the very small *Trematomus* type otoliths that were categorised as juvenile fish. Channichthyid, eroded and juvenile fish otoliths had no distinct features by which to make species-specific identifications. To estimate mass, channichthyid otoliths were measured and assumed to be *Chaenodraco wilsoni* (a medium size channichthyid and a common constituent of the diet of predators in Prydz Bay, Williams & McEldowney 1990). Similarly, for the purposes of mass estimates, both juvenile fishes (estimated standard length 7 cm) and eroded otoliths (estimated average length of uneroded *T. bernacchii* otoliths) were assumed to be *T. bernacchii* (a common species of benthic fish in inshore habitat, Eastman 1993).

Cephalopod taxa were identified and quantified by lower beaks with reference to (Clarke 1986, Daly and Rodhouse 1994, Allcock and Piernney 2002) and a collection vouched for by M. Clarke located at the Australian Antarctic Division, Tasmania. Squid lower-beak rostral lengths and octopus lower-beak hood lengths were measured using digital vernier callipers. The mass of *Psychroteuthis glacialis* was estimated using an allometric equation from Gröger et al. (2000). Except for *Pareledone polymorpha* (Daly & Rodhouse 1994, Allcock & Piernney 2002), there were no distinguishing features by which to group the octopus lower beaks into different taxa. Initially, it was assumed that all octopus lower beaks not identified as *P. polymorpha* were actually *P. turqueti*, and mass was estimated using Figures in Daly & Rodhouse (1994). However, the resulting estimate of 250 g per octopus was large compared to observations of octopus from Weddell seal regurgitates (S. Lake unpubl. data), the masses of octopus in Weddell seal diet estimated by Casaux et al. (1997), and also the relatively small mantle lengths described by Allcock et al. (2001). Considering this, I made a general estimate for octopus body mass at 100 g.

Prawn taxa were identified and quantified by number using their carapaces with reference to Kirkwood (1983). Prior to this study there were no published allometric equations for estimating the body mass (BM) of these prawn species from carapace length (CL). To address that problem, bait traps were set in Ellis Fjord (Vestfold Hills) and CL and BM were measured for each of the 35 *Chorismus antarcticus* caught in the traps. CL ranged from 6 to 16 mm. The best-fit regression formula was an exponential function:  $BM = 0.000943(CL)^{2.976}$ ,  $R^2 = 0.976$  (Figure 2-2). The same allometric equation was used to estimate the BM of *Notocrangon antarcticus* because the 2 prawn species have a similar morphology (Kirkwood 1983). The BM of mysids was assumed to be equivalent to the wet mass of mysid exoskeletons in processed scats. Mysid exoskeletons were mainly intact and, flooded

with water, the mass of exoskeletons would have been similar to the undigested mass of these small-bodied crustaceans.

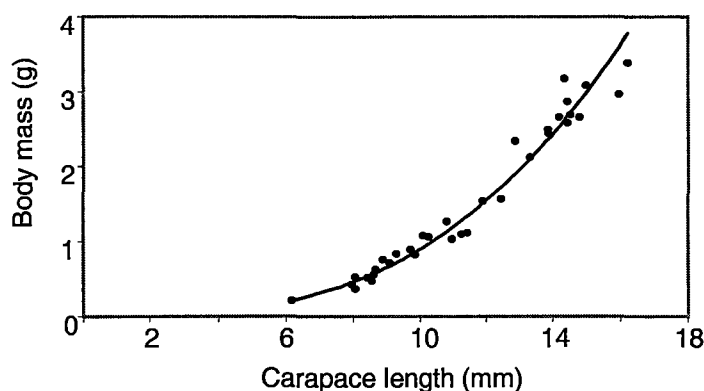


Figure 2-2 *Chorismus antarcticus*. Regression equation relating carapace length (CL) to body mass (BM) for 35 prawns caught in traps at the entrance to Ellis Fjord, Vestfold Hills (see Figure 2-1c)

### *Study areas and sampling design*

At the Vestfold Hills (68° 33' S, 78° 15' E, Figure 2-1), the distribution of Weddell seals changed from breeding sites in spring to moulting sites in summer (see Green et al. 1995). Long Fjord was the main breeding area, where approximately 100 pups suckled from October to December. The Tryne area was also used for breeding (40 pups per annum); but mainly for moulting as several hundred seals aggregated in this area from January to March each year. Breeding aggregations included mother-pup pairs and seals without pups of both sexes. Overall, 56% of the Vestfold Hills spring sample was from breeding colonies and the remainder was from non-breeding sites throughout the fast ice areas. In spring at the Vestfold Hills, over-snow vehicles were used for transport and the main constraint to sampling was paucity of scats in the Tryne area. In summer, after most of the sea ice had melted, helicopters were used for transport and this was possible in 1995 and 1996 only. At Mawson (68° 00' S, 63° 00' E, Figure 2-1), helicopters were not available. A regular sampling regime was maintained throughout winter (April to September) and spring in both 1996 and 1997 but not in summer of either year. One third of the Mawson spring sample was from breeding colonies. At the Larsmann Hills (69° 24' S, 76° 13' E, Figure 2-1), a sample was obtained from Thala Fjord in January 1996. At Commonwealth Bay (67° 00' S, 142° 30' E, Figure 2-1), a sample was obtained from Boat Harbour in January 1997. Analysis of variation between breeding colonies within Long Fjord in 1993, was originally reported by Lake (2000) and included here for analysis of within sample variability.

*Data analysis*

Frequency of occurrence described the rate at which prey types were targeted (Table 2-1). Number of prey remains conveyed additional information about the relative proportions of prey in the diet. Estimates of mass took into account the number and also size of prey to describe species' contributions to the diet. However, the estimate of octopus mass was imprecise and this would have affected the relative mass of other prey types. To minimise this inaccuracy, the statistical analyses was of numerical data and test results were simply interpreted with regard to body mass of prey (Table 2-2). Diet composition was compared by randomization (Manly 1997) and parametric methods (Johnson and Field 1993). Both tests were performed in S-Plus (Insightful Applications) using matrices of number of each prey species per scat. Randomisation tests bound the columns (prey species) while randomising the rows (sample labels). Two-way randomisation tests were conducted as separate 1-way analyses, where one factor was held constant (e.g. year) while the other factor (e.g. location) was randomised, and vice versa. Under the null hypothesis, the randomised factor was not significant in determining the diet. The steps to randomization were (a) calculating the F-statistic for observed data, (b) randomising the labels 5000 times to calculate the distribution of the F-statistic under the null hypothesis, and (c) comparing the F-statistic of the observed difference with the distribution of F under the null hypothesis. If the null hypothesis was true then the observed value of F was within the distribution of 95% of the Fs calculated from random allocation. This approach made few assumptions about the data (Manly 1997) but did not test for interaction effects. Parametric tests were done by MANOVA (multivariate analysis of variance) using Type-1 sums of squares. The assumptions of MANOVA were multi-normality of error terms and homogeneity of group co-variances (Johnson & Field 1993). In this case, the data were not homoscedastic or normally distributed for any of the prey types, and could not be transformed as such because of the large number of zeros. Although it was inappropriate to ignore the assumptions, it was equally improper to reject the test as invalid since many statistics are robust to violations of their theoretical requirements (Johnson & Field 1993). The randomization tests and MANOVA gave similar results, although randomisation procedures yielded more conservative significance levels. The results from randomization have been quoted unless the results of the 2 tests differed, in which case both results are given. Univariate versions of the same tests (with  $\alpha$ -levels of  $p = 0.05$ ) were used to interpret the results of multivariate tests. Prior to analysis, the data were reduced according to a criterion of percentage dominance (Field et al. 1982). By this method, all species with frequency of occurrence greater than 10% in at least one sample collection were retained. Four species of benthic fish did not meet the criterion: *Pagothenia hansonii*, *Trematomus centronotus*, *Notothenia kempfi* and *N. neglecta* (Table 2-1). These species were not abundant in any of the samples.

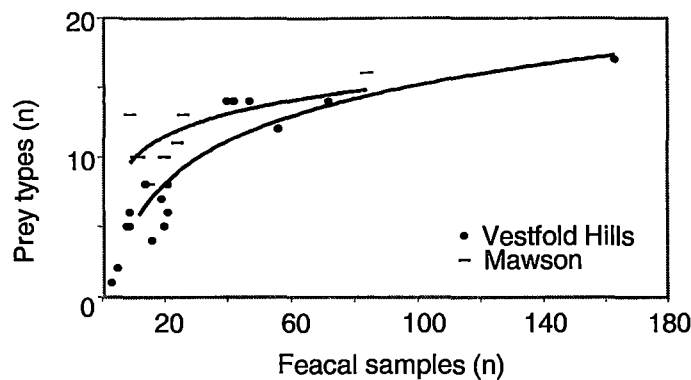


Figure 2-3 *Leptonychotes weddelli*. Number of prey types relative to the number of samples, in faecal samples from the Vestfold Hills and Mawson.

### RESULTS

Number of species in the diet was related to number of scats in the sample (Figure 2-3): About 10 prey types were described from 15 to 25 scats whereas about 14 prey types were described from 40 to 60 scats. Sample sizes for different areas, seasons and years varied from 8 to 163 scats, and this was a potential source of variation in the diet descriptions. However, the statistical techniques compared number of individuals per species per scat rather than the average number of individuals per species per sample. Furthermore, rare species were eliminated prior to analysis to avoid coincidental co-occurrence of rare species dominating the results. In these ways, variation in diet due to irregular sample sizes was minimised; but this source of variation should still be considered with regard to number of prey species described in the diets, and the reliability of quantitative estimates for prey species that occurred infrequently in the samples (Figure 2-3).

Table 2-1 *Leptonychotes weddelli*. Diet at Commonwealth Bay (CB), Larsemann Hills (LH), Mawson (M) and the Vestfold Hills (VH) described by frequency of occurrence (%), mean number of prey per scat, mean mass of prey per scat and percentage of total estimated mass of prey in the diet (<0.5 = '0', not detected = '-'). Samples were from summer 1996 at CB (86 scats), summer 1997 at LH (29 scats), winter and spring 1996-97 at M (201) and spring and summer 1992-96 at VH (585 scats)

	Frequency of occurrence (%)				Mean no, prey per scat				Mean mass prey per scat (g)				Proportion total mass (%)			
	CB	LH	M	VH	CB	LH	M	VH	CB	LH	M	VH	CB	LH	M	VH
<b>Fish (total)</b>	13	39	60	39	2	4	13	6	64	53	157	114	60	75	17	68
<i>Pleuragramma antarcticum</i>	6	27	41	8	1	2	10	3	25	38	62	11	23	54	7	7
Juvenile fish	-	15	18	7	-	1	1	1	-	5	6	6	-	7	1	4
Eroded benthic otoliths	7	9	11	14	0	0	0	1	18	8	24	53	16	11	3	32
<i>Aethotaxis mitopteryx</i>	-	-	0	-	-	-	0	-	-	-	1	-	-	-	0	-
Channichthyidae	1	3	10	2	0	0	0	0	0	1	15	2	0	2	2	1
<i>Dissostichus mawsoni</i>	1	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
<i>Lepidonotothen kemp</i>	-	-	1	2	-	-	0	0	-	-	0	1	-	-	0	1
<i>Notothenia coriiceps</i>	-	-	0	0	-	-	0	0	-	-	0	0	-	-	0	0
<i>Pagothenia borchgrevinkii</i>	1	-	1	4	0	-	0	0	0	-	1	4	0	-	0	2
<i>Trematomus bernacchii</i>	1	-	2	13	0	-	0	1	8	-	3	16	8	-	0	9
<i>Trematomus eulipidotus</i>	-	-	2	0	-	-	0	0	-	-	3	0	-	-	0	0
<i>Trematomus hanson</i>	-	3	-	0	-	0	-	0	-	1	-	0	-	1	-	0
<i>Trematomus lepidorbinus</i>	-	-	3	1	-	-	0	0	-	-	8	1	-	-	1	1
<i>Trematomus loenbergi</i>	-	-	1	1	-	-	0	0	-	-	1	3	-	-	0	2
<i>Trematomus newnesi</i>	1	-	4	2	0	-	0	0	12	-	29	8	11	-	3	5
<i>Trematomus pennellii</i>	1	-	2	3	0	-	0	0	0	-	5	3	0	-	1	2
<i>Trematomus scotti</i>	2	-	1	8	0	-	0	0	1	-	0	6	0	-	0	4
<b>Cephalopod (total)</b>	17	6	56	9	0	0	7	0	38	10	756	31	36	14	82	18
<i>Pareledone polymorpha</i>	-	-	2	-	-	-	0	-	-	-	7	-	-	-	1	-
<i>Pareledone</i> spp-	17	3	41	8	0	0	3	0	38	6	343	27	36	8	37	16
<i>Psychroteuthis glacialis</i>	-	3	36	1	-	0	3	0	0	4	406	4	-	5	44	2
<b>Prawns (total)</b>	24	6	18	35	2	0	1	8	4	1	1	57	4	1	0	34
<i>Chorismus antarcticus</i>	24	3	15	33	2	0	0	6	4	1	1	14	4	1	0	8
<i>Notocrangon antarcticus</i>	-	3	5	9	-	0	0	2	-	0	1	6	-	0	0	3
<b>Mysid</b>	1	15	21	6	-	-	-	-	1	8	11	3	0	11	1	2
<b>Total</b>	63	84	217	122	4	4	20	15	107	71	925	167	100	100	100	100



Table 2-2 *Leptonychotes weddelli*. Prey size (mean, SD and median in brackets), estimated from the lengths of undigested diagnostic remains recovered in 905 scats. Data are standard lengths for fish, mantle lengths for cephalopods and total lengths for prawns. Allometric equations from Williams and McEldowny (1990) or as specified. Data are not presented if no allometric equation.

Prey type (n)	Length of prey remains (mm)	Length of prey (mm)	Mass of prey (g)
<b>Fish</b>			
<i>Aethotaxis mutopteryx</i> (2)	0.1		80.0
Channichthyidae (26)	1.7 +/- 0.1 (1.7)	163.7 +/- 4.2 (164.4)	42.0 +/- 3.8 (40.0)
<i>Lepidonotothen kemp</i> i (15)	3.5 +/- 0.9 (3.5)	112.9 +/- 54.3 (110.6)	36.7 +/- 46.5 (18.8)
<i>Notothenia coriiceps</i> (3)	2.8 +/- 0.5 (2.5)	211.5 +/- 37.1 (190.8)	216.2 +/- 139.6 (154.5)
<i>Pagothenia borchgrevink</i> i (14)	2.4 +/- 0.5 (2.4)	146.6 +/- 44.8 (147.2)	66.3 +/- 55.1 (51.8)
<i>Pleuragramma antarcticum</i> (1 972)	1.0 +/- 0.2 (1.0)	93.1 +/- 17.4 (91.1)	6.1 +/- 5.2 (5.1)
<i>Trematomis hanson</i> i (2)	2.3 +/- 0.6 (2.3)	100.4 +/- 32.5 (100.4)	15.6 +/- 16.8 (15.6)
<i>Trematomus bernacch</i> ii (263)	2.9 +/- 0.7 (2.9)	115.0 +/- 32.0 (113.4)	26.2 +/- 24.9 (19.8)
<i>Trematomus eulepidotus</i> (2)	3.9 +/- 0.2 (3.9)	201.3 +/- 10.4 (201.3)	162.3 +/- 45.8 (162.3)
<i>Trematomus lepidorhinus</i> (11)	4.2 +/- 0.8 (4.1)	195.9 +/- 35.7 (191.6)	147.4 +/- 86.2 (122.5)
<i>Trematomus newnes</i> i (50)	2.4 +/- 0.4 (2.4)	178.6 +/- 20.8 (178.7)	96.9 +/- 34.4 (93.0)
<i>Trematomus pennell</i> i (65)	3.5 +/- 0.6 (3.4)	113.6 +/- 23.8 (110.8)	30.5 +/- 21.1 (24.3)
<i>Trematomus scott</i> i (50)	3.4 +/- 1.0 (3.5)	86.4 +/- 21.7 (88.3)	11.6 +/- 9.4 (9.8)
<b>Cephalopods</b>			
<i>Pareledone polymorpha</i> (7)	5.4 +/- 1.1 (5.1)		
<i>Pareledone</i> spp. (396)	8.7 +/- 3.1 (8.4)		
<i>Psychroteuthis glacialis</i> (248)	3.4 +/- 2.0 (2.3)	93.6 +/- 141.8 (9.8)	**123.0 +/- 83.3 (76.4) **
<b>Crustaceans</b>			
<i>Chorismus antarcticus</i> (2 072)	13.9 +/- 1.7 (13.8)	74.2 +/- 8.3 (73.8)	2.4 +/- 0.6 (2.4) *
<i>Notocrangon antarcticus</i> (442)	14.3 +/- 2.4 (14.1)	71.2 +/- 10.6 (70.2)	2.6 +/- 0.8 (2.5) *

\* mass = 0.3529 x carapace length - 2.4824

\*\* Arntz and Gorny (1991)

*Spring diet at the Vestfold Hills*

The finest scale examined in this study was within Long Fjord in 1994 (Figure 2-1d). Scats from 3 colonies were compared in October (19, 19 and 31 scats per colony) and December (17, 18 and 31 scats per colony). Both randomisation and MANOVA indicated that variation between pupping colonies was not significant ( $F_{4,122} = 0.70$ ,  $p = 0.16$ ), and neither was variation over time ( $F_{3,121} = 0.77$ ,  $p = 0.18$ ). On a broader scale, the Vestfold Hills' spring diet was described from 423 scats collected between 1992 and 1995. The majority (70%) of the spring collection was from Long Fjord (47, 42, 163 and 40 scats per year, from 1992 to 1995 respectively). The Tryne area was sampled irregularly due to paucity of scats (8, 30, 0 and 8 scats). The rest of the spring collection was from oceanic areas where non-pupping seals hauled out (0, 20, 56 and 9 scats). Overall, 65% of scats had evidence of prey; on average there was evidence of 12.7 prey per scat, and 17 different prey types were identified.

Within the spring diet (Figure 2-4), both randomization and MANOVA showed significant effects for location ( $F_{6, 419} = 0.72$ ,  $p = 0.04$ ) and for year ( $F_{7, 420} = 0.72$ ,  $p = 0.02$ ). Univariate randomisations suggested that the location effect was due to *Trematomus bernacchii* occurring exclusively in Long Fjord samples. Prawns *Chorismus antarcticus* and *Notocrangon antarcticus* were also relatively abundant in the Long Fjord samples. *Pleuragramma antarcticum* occurred mainly in samples from the Tryne area. Inter-annual differences were attributed to prawns and juvenile fish; however, both these prey types were abundant yet small, thus dominating numerical tests more than diet composition.

*Summer diet at the Vestfold Hills*

The summer diet (Figure 2-5) at the Vestfold Hills was described from 163 scats collected in 1995 and 1996. Most of the summer collection was from the Tryne area (35 and 86 scats per year). There were also 20 scats from Ellis Fjord in 1995, and 21 scats from Long Fjord in 1996. Overall, 53% of scats contained evidence of prey; on average there was evidence of 8.2 prey per scat, and 14 different prey types were identified. This was slightly less prey than quantified at the Vestfold Hills in spring.

Both randomisation and MANOVA indicated that location was a significant determinant of the summer diet at the Vestfold Hills ( $F_{2,160} = 0.68$ ,  $p < 0.00$ , Figure 2-5). As in spring, both prawn species were relatively abundant in the Long Fjord sample. In summer, *Chorismus antarcticus* was relatively abundant in the Ellis Fjord sample too. Inter-annual variation was not significant in summer at the Vestfold Hills ( $F_{1,160} = 0.92$ ,  $p = 0.44$ ). However this may be an overly conservative result since the data was limited to 2 yr and the Tryne area only. Similarly, tests indicated that seasonal variation was not significant in the Vestfold Hills diet ( $F_{1,167} = 0.89$ ,  $p = 0.06$ ). However, this comparison was

limited to the Tryne area only, where 3 yr were sampled in spring and 2 in summer. With this sample collection, seasonal variation in the diet of seals could not be evaluated in a satisfactory way.

### *Winter and spring diets at Mawson*

Spring diet at Mawson was described from 58 scats, including 9 scats from the central coast in 1996, and 26, 11 and 12 scats from the east, west and central coasts in 1997 (Figure 2-1). In spring, 90% of scats contained prey remains; on average there was evidence of 20.4 prey per scat, and 14 prey types were identified. For winter, the diet at Mawson was described from 143 scats, including 15 scats from the central coast in 1996, and 24, 21 and 84 scats from east, west and central areas in 1997. In winter, 73% of scats contained prey remains; on average there was evidence of 10.6 prey per scat, and 15 taxa were identified. This was more prey by number and mass than evidenced in the diet at the Vestfold Hills (Table 2-1).

The difference between winter and spring diets at Mawson was significant by both randomisation and MANOVA ( $F_{1,200} = 0.82$ ,  $p < 0.00$ ). This was attributed mainly to *Psychroteuthis glacialis* and *Trematomus bernacchii* being more abundant in spring. Overall, *P. glacialis* was the dominant prey type (44% mass, Table 2-1). *T. bernacchii* was relatively unimportant in the Mawson diet (<1% mass). *P. glacialis* was abundant in scats from September to November in both years, with a bimodal distribution of size-classes (Figure 2-6). The larger size-class disappeared from the diet in October 1996 and in November 1997. With regard to octopus, apart from *Pareledone polymorpha*, the octopus beaks in the Mawson diet had a normal length-frequency distribution, suggesting that they represented a single species. Inter-annual variation in the Mawson diet was significant by MANOVA ( $F_{1,195} = 2.61$ ,  $p > 0.00$ ) but not by randomisation ( $F_{3,198} = 0.57$ ,  $p = 0.08$ ). This ambiguous result could reflect the different sample sizes used to represent 1996 compared to 1997. The effect of location was not significant in Mawson diet, either by randomization or MANOVA ( $F_{4,199} = 0.56$ ,  $p < 0.11$ ).

### *Regional comparisons*

The Vestfold Hills and Mawson diets, compared in spring, were significantly different by both randomization and MANOVA tests ( $F_{1,480} = 0.65$ ,  $p < 0.00$ ). There were significantly more channichthyds, *Pleuragramma antarcticum*, *Trematomus newnesi*, squid (*P. glacialis*) and octopus in the Mawson diet, and more *T. bernacchii* and *Chorismus antarcticus* in the Vestfold Hills diet. At Mawson, a large proportion of scats contained evidence of prey remains and multiple prey types occurred commonly in the same scat (Figure 2-7). Overall, more prey was represented in scats from Mawson (Table 2-1).

Summer diets were described for Commonwealth Bay in 1997 (87 scats) and Larsemann Hills in 1996 (29 scats), as well as the Vestfold Hills in 1995 and 1996 (Figure 2-5). Paucity of prey distinguished the Commonwealth Bay and Larsemann Hills collections (2.8 and 2.4 prey per scat respectively) from the Vestfold Hills collection (8.2 prey per scat). While randomisation tests showed that variation between these collections was not significant ( $F_{2, 281} = 0.89$ ,  $p < 0.16$ ), MANOVA showed a significant effect ( $F_{3, 276} = 0.65$ ,  $p < 0.00$ ) due to prawns being more abundant at the Vestfold Hills and Commonwealth Bay.

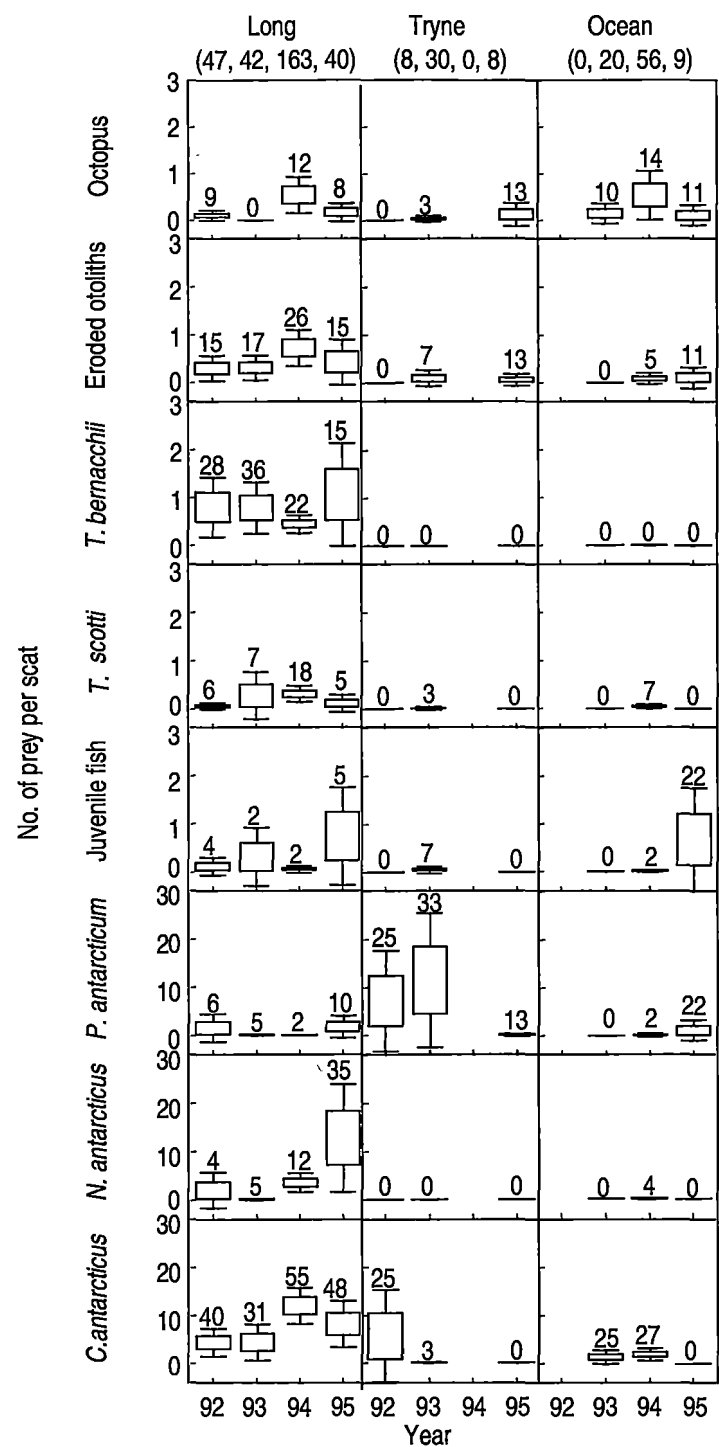


Figure 2-4 *Leptonychotes weddellii*. Temporal and spatial variation within the spring diet at the Vestfold Hills (Long Fjord, Tryne area and Ocean). Numerical abundance of each prey type is shown by a box of 1 SE around the mean, with whiskers at 95% CIs. Frequency of occurrence (%) is given above each plot, and number of scats per sample is listed in brackets after location.

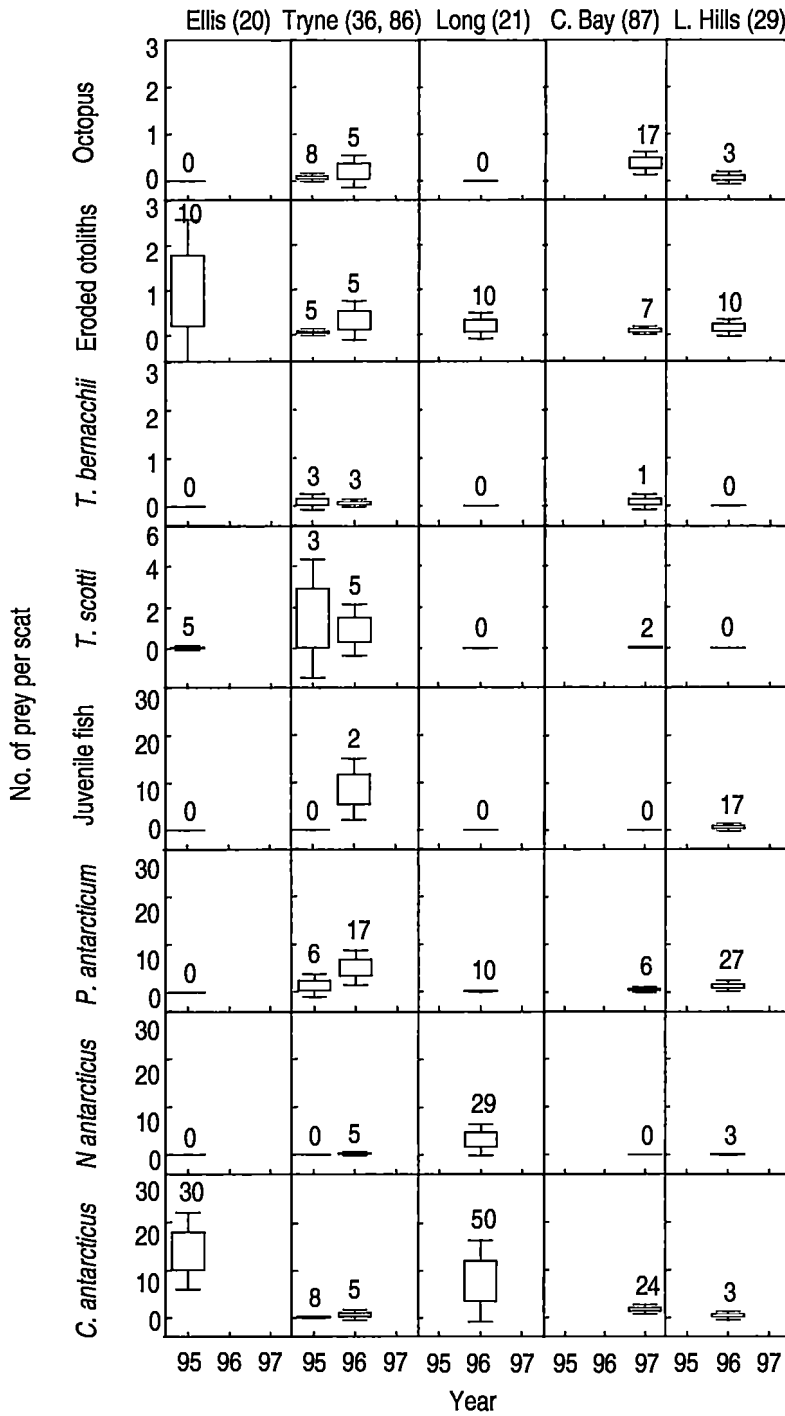


Figure 2-5 *Leptonychotes weddellii*. Temporal and spatial variation within the summer diet at Vestfold Hills (Ellis Fjord, Tryne area and Long Fjord), and also at Commonwealth Bay (C. Bay) and Larsemann Hills (L. Hills). Numerical abundance of each prey type is shown by a box of 1 SE around the mean, with whiskers at 95% CIs. Frequency of occurrence (%) is given above each plot, and number of scats per sample is listed in brackets after location.

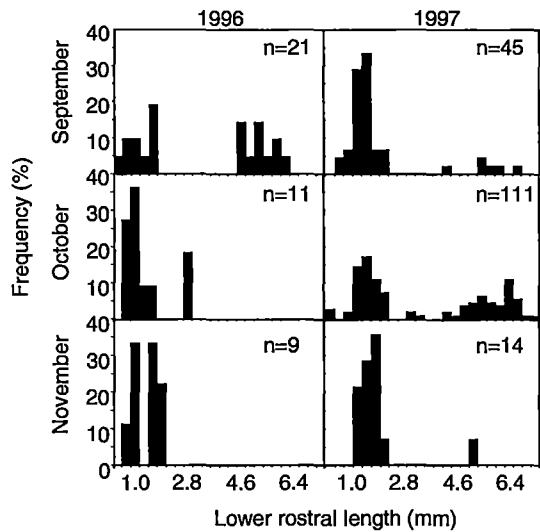


Figure 2-6 *Psychroteuthis glacialis*. Length frequency distribution evidenced by rostral lengths of lower beaks in scats from Mawson, September to November of 1996 and 1997

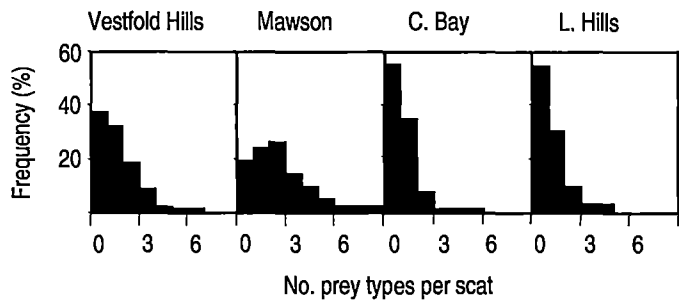


Figure 2-7 *Leptonychotes weddelli*. Number of prey types recovered per scat, where numbers varied from zero identifiable prey to 8 different prey types occurring in the same scat.

## DISCUSSION

### *Caveats on the data*

Feeding trials have shown that using scats to estimate prey composition yields biased results because prey remains are differentially digested (Pierce and Boyle 1991, Lake 1997, Staniland 2002). Fish otoliths are more susceptible to digestion than cephalopod beaks and prawn exoskeletons. Thus abundance and perhaps size of fish is underestimated relative to other prey types. Severity of digestion varies according to predator species, prey species, meal size, prey size and predator behaviour (Bowen 2000). Weddell seal digestion appears to be relatively severe, perhaps due to ingestion of substrate similar to other benthic foragers, such as Australian sea lions *Neophoca cinerea* (Gales and Cheal 1992). Sand was in 44% of scats, and stones in 14% of scats, which probably contributed to mechanical digestion. In this case, the substrate must have come from the gut because scats were collected from sea ice. Feeding trials specific to Weddell seals have not been conducted because there are no Weddell seals in captivity, but severity of digestion is evident from the low numbers of otoliths recovered from scats, specifically no otoliths at all (Testa et al. 1985), 0.81 otoliths per scat (Green and Burton 1987) and 0.95 otoliths per scat (Burns et al. 1998). However, conclusions about changes in diet are still valid, assuming that biases remain constant. This assumption may be incorrect when the severity of digestion increases due to small meal sizes and thus reduced passage rates during the moulting and breeding haul-out periods (Marcus et al. 1998). This is discussed with regard to differences in the overall abundance of prey evident in the samples.

Other potential biases include non-representative sample collections, consumption of prey without hard parts, and statistical power in detecting variability. Scats represent approximately 1 day of feeding (Bowen 2000) and all of our scats were from coastal areas so the diet descriptions are likely to be biased towards coastal prey species. Larger fish, such as some channichthyid species or *Dissostichus mawsoni*, were not evident in the diet but they may have been consumed and the heads not eaten (Pierce & Boyle 1991). Finally, the power of some comparisons was limited. For example, the seasonal comparison at the Vestfold Hills was limited to the Tryne area, with 35 and 86 scats per year in summer compared with 8, 30 and 8 scats per year in spring. Lack of significant differences may have reflected small sample sizes and thus statistical power, rather than lack of change in the diet. This is in addition to 8 scats being a less than adequate replicate sample (Figure 2-3).

This study described the diet at the Vestfold Hills and Mawson, as did Green & Burton (1987). The earlier report differed mainly with regard to *Trematomus scotti*. Despite *T. scotti* being a common fish species with very distinctive otoliths, this is the first report to identify *T. scotti* in the diet of any Antarctic predator (Williams & McEldowney 1990). By retrieving otoliths from archives and checking identifications we found that Green & Burton (1987) referred to *T. scotti* as *Nototheniidae*



sp. 1, and *T. newnesi* as Nototheniidae sp. 2. Thus these findings were consistent with the previous report.

### *Vestfold Hills*

Spatial variation in the diet of Weddell seals at the Vestfold Hills seemed to reflect different marine ecotypes within the fjords and bays, consistent with the findings of Dhargalkar et al. (1988), who attributed distribution of macro-algae species to different degrees of exposure to ocean currents. Within each ecotype, the seals' diet was relatively consistent (Figs. 2-4 & 2-5). In Long and Ellis Fjords the diet contained prawns in quantities greater than in other regions of Antarctica (Plötz et al. 1991, Burns et al. 1998, Plötz et al. 2001), yet this was consistent with the previous report for the Vestfold Hills (Green & Burton 1987). Benthic fish, particularly *Trematomus bernacchii*, were also relatively abundant in Long Fjord. High levels of secondary biomass have been described in these fjords and attributed to complex bathymetry and active tidal regimes, resulting in areas of rapid water flow and thus enhanced plankton 'pass by' flux (Kirkwood and Burton 1988). Rapid water flow sustains tubeworm reefs that are substrate for populations of benthic prawns. Both prey availability and the seals' functional response (Bowen et al. 2002) determine diet composition. Weddell seals in the southern fjords of the Vestfold Hills seem accustomed to foraging on small benthic prey.

Localised prey resources could result in seals choosing sequential foraging locations according to prey availability. After the seals deplete benthic prey in Long Fjord in spring, they could harvest pelagic prey in the Tryne area in summer. The diet in the Tryne area was characterised by the pelagic fish *Pleuragramma antarcticum*, which feed on krill, which in turn feed on algae that bloom in summer as the ice melts (Plötz et al. 2001). The Tryne area is on the northern side of the Vestfold Hills (Figure 2-1) and opens into the flow of the Prydz Bay gyre (Smith and Treguer 1984). Thus prevailing currents could bring *P. antarcticum* into Tryne Bay and Tryne Fjord. There were few and oscillating numbers of prey evident in the scats from offshore areas (Figure 2-4), despite seals in offshore areas apparently being free of breeding constraints. The relatively high numbers of prey in scats from the fjords indicated that the fjord ecotypes at the Vestfold Hills were good foraging habitats, at least when they were sampled in spring and summer.

### *Mawson*

The Mawson diet was spatially homogeneous compared to the Vestfold Hills. Hypothetically, the proportion of benthic to pelagic prey should increase in shallow water because benthic prey is more

accessible (Tremblay and Cherel 2000). However the diet of seals over the shallow bank to the east of Mawson did not contain more benthic prey than the diet of seals in the vicinity of the central or western troughs (Figure 2-1). The phenomena of Eckman drift (Pond and Pickard 1983) whereby southward flowing currents reach the coast and deflect west, could be the mechanism causing spatial homogeneity in the Weddell seal diet. Alternatively, there may be overlap in the foraging areas of seals at different haul-out sites (Figure 2-1). Robertson (1995) found spatial differences in the diet of emperor penguins *Aptenodytes forsteri* at Mawson, but this result was tentative due to small sample sizes and asynchrony of sampling.

The Mawson diet varied significantly between winter and spring, mainly with regard to the squid *Psychroteuthis glacialis*, which was relatively abundant in spring. Even within spring there were changes over time in the squid consumed (Figure 2-6). In September, 2 size-classes were abundant in the diet, representing individuals of 3 to 20 g and 230 to 600 g body mass (Gröger et al. 2000). The larger size-class dropped out of the diet in October 1996 and November 1997. Diminishing representation of the larger size-class could have been related to changes in squid distribution, changes in seal foraging distribution, squid stock depletion by predators, or senescence of squid after a prolonged spawning period in late winter and early spring (Lu and Williams 1994). The 2 size-classes were probably from different habitats; small *P. glacialis* being pelagic and large *P. glacialis* having a demersal existence in deeper waters (>450 m) (Jackson and Lu 1994). At the Mawson coast, there may be suitable habitat for large *P. glacialis* on the slopes of the underwater canyons (Figure 2-1). Like prawns at the Vestfold Hills, squid was a fluctuating food source. Whereas prawns were small (~2.5 g), squid were large (~100 g) and thus a substantial additional prey source (Figure 2-7) that became available to the seals around the time of pupping on the Mawson coast.

*Pleuragramma antarcticum* is a keystone species in Antarctic continental shelf ecosystems (Fuiman et al. 2002). The abundance of *P. antarcticum* may fluctuate with environmental conditions more so than other species because it is pelagic and so utilises water column production directly (Hubold and Ekau 1987). *P. antarcticum* occurred in less than half the samples at Mawson despite its high abundance in the diet (Table 2-1). This probably reflected a clumped distribution at any point in time as shoals of this fish are known to wander slowly in and out of sampling areas (Fuiman et al. 2002) and thus be encountered episodically by the seals. Since there is high variability in the abundance of *P. antarcticum* in scats, a large sample size is required to detect characterize it's consumption. In this study, interannual variation in *P. antarcticum* was not significant at either Mawson or the Vestfold Hills. However the comparisons were limited to only 2 yr, except in Long Fjord where *P. antarcticum* was not an important prey type. This study showed that *P. antarcticum* was an important prey type at Mawson, and that spatial homogeneity in the Mawson diet would permit inference from discrete samples to the

whole ecosystem. Future investigation of temporal variation in *P. antarcticum* would be most worthwhile using scats from Mawson.

There was also a large amount of cephalopods in the diet at Mawson, and this was consistent with the previous report of the Weddell seal diet at Mawson based on 18 scats (Green & Burton 1987). It was also consistent with the emperor penguin diet having more cephalopods at Mawson than at other locations in east Antarctica (Robertson 1995). In Weddell seal diet, abundance of cephalopods was markedly higher at Mawson (82% mass, Table 2-1) than at the Vestfold Hills (2%), Larsemann Hills (2%), and Commonwealth Bay (10%), and at other sites around the Antarctica continent (4 to 21% mass, Plötz 1996, Castellini et al. 1992, Burns et al. 1998). The only location, apart from Mawson, where Weddell seal diet had a large component of cephalopods was the South Shetland Islands in the Scotia Arc, sub-Antarctica (91% mass, Casaux et al. 1997). As fish predators (Roper et al. 1985, Daly & Rodhouse 1994), cephalopods represent another level of complexity in the food web. The fish biomass in the Scotia Arc is an order of magnitude greater than is generally the case over the Antarctic continental shelf, in the Weddell Sea for example (Hubold 1991). The abundance of *Pleuragramma antarcticum* in Weddell seal scats (Table 2-1) was also evidence of relatively high fish biomass at Mawson, similar to the Scotia Arc. Perhaps the Mawson food web, which appears relatively complex for the presence of cephalopods, is enriched by relatively warm, circumpolar deep water advected through the deep underwater canyons from the ocean shoreward of the continental slope (Figure 2-1).

### *Regional comparisons*

There were striking differences between regions in the number of prey evident in scats. In summer, Larsemann Hills and Commonwealth Bay averaged 2 prey per scat compared to 8 prey per scat at the Vestfold Hills at the same time of year (Figure 2-5). Sizes of prey taken at the Larsemann Hills and Commonwealth Bay were not larger than at the Vestfold Hills (Table 2-2). Thus the difference in number of prey was not accounted for by prey size. Marcus et al. (1998) showed that fasting seals have more intense digestion. Paucity of prey remains could therefore indicate that the seals were eating less food. It could also indicate consumption of soft-bodied prey, such as holotherians and salps, but there was no direct evidence for this. Considering that seals were hauled out in dense aggregations on small areas of remnant fast ice for moulting, I suggest the paucity of prey remains in scats from Commonwealth Bay and Larsemann Hills (Figure 2-5) was the result of seals foraging less successfully at these locations.

Similarly during spring, when Weddell seals breed, the number of prey evident in scats was greater at the Vestfold Hills and at Mawson than at McMurdo Sound (Testa et al. 1985, Burns et al. 1998) or in

the Weddell Sea (Reijnders et al. 1990). While non-breeding animals probably contributed to sample collections, it is unlikely that they were solely responsible, as 33 to 56% of the spring sample in this study was from breeding colonies. If breeding females were not successful in their foraging at the Vestfold Hills and Mawson then a larger proportion of scats would have had few or no prey remains. Sato et al. (2002) discuss how Weddell seals fast or forage during lactation depending on whether prey are available. Results from this study suggest that seals at both the Vestfold Hills and Mawson were feeding to some extent during lactation, more than at McMurdo Sound (Hindell et al. 2002).

Plötz et al. (2001) suggested a hunting seal descending from the sea surface would not switch to benthic foraging as long as *Pleuragramma antarcticum* was available in the upper water column. However, travel time to the benthic foraging zone would be negligible in shallow water ecosystems. This could account for the high ratio of benthic to pelagic fish (8.8:1) in the Vestfold Hills diet. At Mawson, the lower ratio of benthic to pelagic fish (1.4:1) (Table 2-1) was in accord with a smaller area of neritic habitat (Figure 2-1). Still, many areas of the Mawson coast are less than 200 m deep, and inshore benthic fish species such as *Trematomus newnesi* were abundant in the diet.

The prey species evident from this study were typical of the Antarctic continental shelf ecosystem. By contrast, in the Weddell Sea, seals took fish species from over the continental slope (Plötz et al. 1991). At the South Shetland Islands, Weddell seals consumed myctophids instead of *Pleuragramma antarcticum*, and benthic fish species from the sub-Antarctic species instead of *Trematomus* spp. (Casaux et al. 1997). Such regional variation in diet demonstrates flexibility of Weddell seal foraging. At McMurdo Sound, *P. antarcticum* was the main prey species (Burns et al. 1998), however multiple prey species seem to be more typical of the Weddell seal diet. Multiple prey species and flexible species composition would minimise the coupling between Weddell seal population dynamics and the dynamics of prey species' availability (Murdoch et al. 2002).

This study is the first report of juvenile notothenid fish (~7 cm) and mysids in the diet of Weddell seals. Previously, small fish and crustaceans were not considered to be an important component of the Weddell seal diet. There is only 1 other report of a Weddell seal eating pelagic crustaceans *Euphausia crystallorophias* (Plötz 1986). Mysids are small crustaceans (5 to 10 mm) that occur in dense swarms. In this study, mysids occurred frequently in scats at all 4 sites (Table 2-1) and in large quantities (up to 1 kg per scat) indicating that the seals were targeting mysid swarms. There is video evidence to suggest that Weddell seals pursue and capture prey as individuals (Davis et al. 1999); however, in the case of mysids the seals may capture several per mouthful. In the oceanic ecosystem, north of the Antarctic continental shelf, krill *Euphausia superba* and myctophids are keystone species (Eastman 1993). Our evidence of small fish and crustaceans in the Weddell seal diet reveals the

potential for Weddell seals to be part of the oceanic community of predators that forage in krill swarms at the southern boundary of the Antarctic Circumpolar Current (Tynan 1999)

### SUMMARY

This description of 905 scats from 4 locations in east Antarctica almost doubles the observations of Weddell seal diet reported to date. Regional, temporal and fine-scale spatial variation in diet was evaluated using both randomisation and parametric statistics. Even within the Vestfold Hills (68° 33' S, 78° 15' E) there were several different ecotypes. In the southern fjords the diet was benthic fish and prawns, whereas in the northern area the diet was dominated numerically by *Pleuragramma antarcticum*—a species of pelagic schooling fish. Along the Mawson coast (68° 00' S, 63° 00' E) the diet was spatially homogeneous but varied over time. Squid *Psychroteuthis glacialis* was an important prey type for a short time in spring, and octopus was also abundant in the Mawson diet. As higher order predators, cephalopods represent another layer of complexity in the food web at Mawson. Both Vestfold Hills and Mawson seemed to be good foraging areas compared with Commonwealth Bay (67° 00' S, 142° 30' E) and Larsemann Hills (69° 24' S, 76° 13' E), where seals appeared to have eaten less during the summer haul-out period. This investigation showed that small crustaceae (mysids) were an important prey type, thus revealing the capacity for Weddell seals to join the krill-feeding communities north of the continental shelf. The variety in diet composition demonstrated both flexibility in the Weddell seals' foraging response and the range of different prey species available to Weddell seals over the Antarctic continental shelf and slope.

# Chapter 3

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## **Spatial utilisation of fast ice by Weddell seals *Leptonychotes weddelli* during winter**

Chapter 3 appears to be the equivalent of the peer-reviewed version of the following article: Lake S, Wotherspoon S, and Burton H. (2005) Spatial utilisation of fast-ice by Weddell seals *Leptonychotes weddelli* during winter. *Ecography* 28: 295-306 which has been published in final form at <http://dx.doi.org/10.1111/j.0906-7590.2005.03949.x> This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.

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### INTRODUCTION

The Earth's climate has been changing since the 1970s at a rate greater than at any time in the last thousand years, and some of the strongest signals have come from polar systems where regional increases in air temperature and extensive melting of ice shelves have been observed (Vaughan et al. 2001). Such changes in the environment necessarily impact resident species, but knowledge of each species' distribution and habitat is needed to identify causal links between population dynamics and the many possible environmental perturbations that could impinge on a species (Croxall et al. 2002). While dynamics of Weddell seal populations have been monitored for the past 30 yr (Testa et al. 1990, Green et al. 1995), this is the first quantitative attempt to characterize the relationship between Weddell seals and fast ice habitat. Similar studies have been conducted by shipboard observation in open water and dynamic ice habitats (Bester et al. 1995, Gelatt and Siniff 1999). However, Weddell seals rarely have been observed in areas accessible to ships. The present study was conducted at the Vestfold Hills (68° S, 78° E) in winter, with the aim of increasing the understanding of the distribution and habitat of Weddell seals, and thus enhancing the ability to interpret population dynamics.

Habitat selection by animals is a complicated process involving several levels of discrimination and a number of potentially interacting factors (Morrison et al. 1992). These factors can be categorised into two types (Leibold 1995). The first type contains those factors determined by intersection of suitable conditions on multiple environmental axes. The other type describes the biological constraints, such as competitors, predators or parasites, which modify the ecological potential into a realised geographical niche. Within fast ice areas of Antarctica, there is probably minimal inter-specific competition or predation that impacts Weddell seals because they are the only air-breathing marine predator specifically adapted to breathe through holes in continuous ice cover. Thus it is proposed that the distribution of Weddell seals in fast ice is determined mainly by environmental variables.

I sought to determine which environmental variables enable Weddell seals to occupy fast ice habitat in winter by developing resource selection functions (Manly et al. 2002) i.e. models that yield values proportional to the probability of use. The process involved mapping the distribution of haul out sites, and developing models to correlate the pattern of occupancy with various environmental gradients. Two types of errors can undermine the accuracy of such models (Fielding and Bell 1997). These are algorithmic errors i.e. limitations imposed by the classification algorithm or data gathering processes, and biotic errors i.e. processes arising directly from the organism's ecology. Biotic errors arise because not all of the ecologically relevant processes are specified in the model, often because the relevant data are unavailable. In this study, the variables used to parameterise distribution were chosen on the basis of available data and with a hope that if they were not directly linked to the

ecology of the species then they would at least be co-linear with variables that were.

For air-breathing, marine predators in the Antarctic, open water can be a limiting resource (Wienecke and Robertson 1997). It takes only a few hours for the ocean surface to freeze in winter, and unless ice-holes are externally generated, Weddell seals have to maintain sites for breathing and hauling out using their teeth. If seals live where constant abrasion of the ice is necessary then tooth wear can become marked over time and may seriously affect a seal's ability to survive (Stirling 1969). Thus it is assumed that the preferred habitat of Weddell seals is where environmental forces crack the fast ice. Cracks form by pressure building up due to atmospheric or oceanic forcing. The pressure is released by fracturing, often between and around obstacles that limit ice movement such as land or ice bergs. Therefore, it was hypothesised that Weddell seal haul out sites are associated with land or ice bergs. Furthermore, thinner ice is more likely to crack than thick, and fast ice thickness in coastal areas varies according to amount of exposure to the relatively warm Circumpolar Deep Water (CDW) (Comiso and Gordon 1987, Heil et al. 1996). CDW penetrates Antarctic coastal environments from the Southern Ocean, and thus there is greater chance of exposure to CDW in deeper water and outer coastal areas. Although highly accurate bathymetry data for the Vestfold Hills is not available, the general trend is for water depth to increase with distance from the coast (Figure 3-1). Therefore, it was hypothesized that distribution of haul out sites could be a function of distance from the coast.

The Vestfold Hills is adjacent to the Sørødal Glacier (Figure 3-1). Deep water seaward of the glacier is associated with a lead of open water that forms immediately adjacent to fast ice and coastal islands in southern Vestfold Hills. The lead penetrates northwest from the Sørødal Glacier along the edge of the broadening strip of coastal fast ice and into Prydz Bay (Michael and Hill 2002). The open-water is a product of several factors. These include depth of water column and thus absence of islands or grounded bergs to anchor the sea ice; shear force of the glacier causing the fast ice to fracture; a clockwise current of dynamic ice gouging southward along the Prydz Bay coast; and high cyclone frequency (atmospheric forcing of the ice) associated with the near stationary low in air pressure in Eastern Prydz Bay. These factors are probably responsible for the small maximum seaward extent of permanent fast ice at the Vestfold Hills (6 - 10 km) (Figure 3-1) relative to other locations in East Antarctica (45-65 km) (Fedetov et al. 1998). Considering this, Worby et al. (1998) recognised the Vestfold Hills as a coastal polynya i.e. an area of recurring open water adjacent to the coast.

Generally, recurring polynyas are important habitat for marine mammals and birds, which depend on their existence at critical times when the ocean is largely ice-covered (Stirling 1997). Polynyas are not only a place where marine mammals and birds can breathe and forage, but also an area of isolation from certain predators and competitors, and possibly an area of increased productivity (Stirling 1997). Polynyas can form either by atmospheric or oceanic forcing. Those formed by atmospheric forcing,



like the Vestfold Hills, are less likely to be associated with increased productivity and an abundance of wildlife. Nevertheless, the distribution of Weddell seal haul out sites at the Vestfold Hills may be influenced by proximity to open water as an area where the seals can breathe, similar to the overwintering distributions of bearded seals *Erignathus barbatus* and walruses *Odobenus rosmarus rosmarus* in the Arctic which is determined largely by the distribution of shore lead systems (Stirling and Cleator 1981). For this reason, I hypothesise that winter distribution of haul out sites could be a function of proximity to the fast ice edge.

## METHODS

### *Field observations*

From May to September in 1999, fast ice areas at the Vestfold Hills were surveyed using Garmin 12xl GPS (Geographical Positioning Systems) to collect data on both seal location and survey track. The surveys were done on 4-wheeled motorbikes, 2 bikes per survey. The people on the bikes searched within line of site of each other, usually ca 300 m apart. The location of one vehicle was recorded at 1.5 min intervals automatically by the GPS. Haul out sites were recognised by the presence of a hole in the ice associated with seals, scats, or imprint marks on the ice surface. A GPS waypoint (latitude and longitude) was recorded at each site, and features of habitat noted. This included diameter of open water in the hole, geography with which the hole was associated (i.e. land, ice berg, ice crack or ice edge), the quantity of scats on the ice and quantity of imprint marks in the snow. Location of the ice edge also was recorded when encountered on survey.

Continuous operation of the GPS was ensured despite temperatures as low as -35°C by mounting the GPS in a heated container on the handlebars of the bike, and powering both the heater and the GPS from the battery of the vehicle. At the time of this study, positional accuracy of non-differential GPS was limited by selective availability of satellites. The precision of instruments was evaluated by measuring the distance between waypoints recorded at the same site on different occasions. There were 8 sets of way points: 4 in Long Fjord, 2 at Plough Island, 1 at Ellis Narrows and 1 in the Hawker Channel (Figure 3-1). The difference within sets of waypoints was  $107 \pm 12$  m ( $n = 14$ ), consistent with the common assumption that selective availability limited GPS accuracy to ca 100 m.

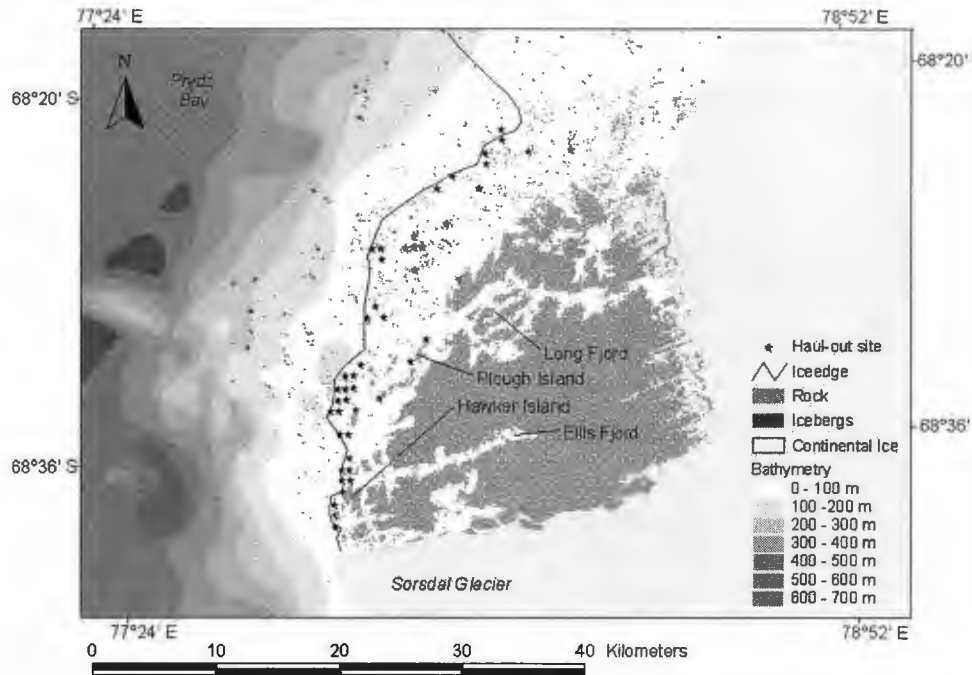


Figure 3-1 The Vestfold Hills, Prydz Bay, East Antarctica, detailing bathymetry to the resolution available for the region (but also see Figure 5-5), in relation to the approximate position of the permanent fast ice edge in September 1999, icebergs as digitized from a satellite image obtained the following summer, and the coast, islands, fjords and continental ice at the Vestfold Hills.

From the beginning of winter, the survey area included fast ice offshore of the mainland and in Long and Tryne fjords but not the two southern fjords (Figure 3-2) because there was no sign of seals when these areas were scanned from hilltops using binoculars. Daylight hours were limited in May, June and July, hence surveys were focused on south, central and fjord regions (Figure 3-2). Longer daylight hours in August and September permitted survey of the northern region as well. Within these constraints, the survey design was repeated each month. The first survey was conducted. Then the track was plotted, gaps in coverage identified, and routes for subsequent surveys planned and followed using waypoints and navigation functions on the GPS. The aim was to achieve approximately even spatial coverage throughout each region. Care was taken not to bias the search area with regard to sea ice terrain. There were 10 - 12 days of survey per month.

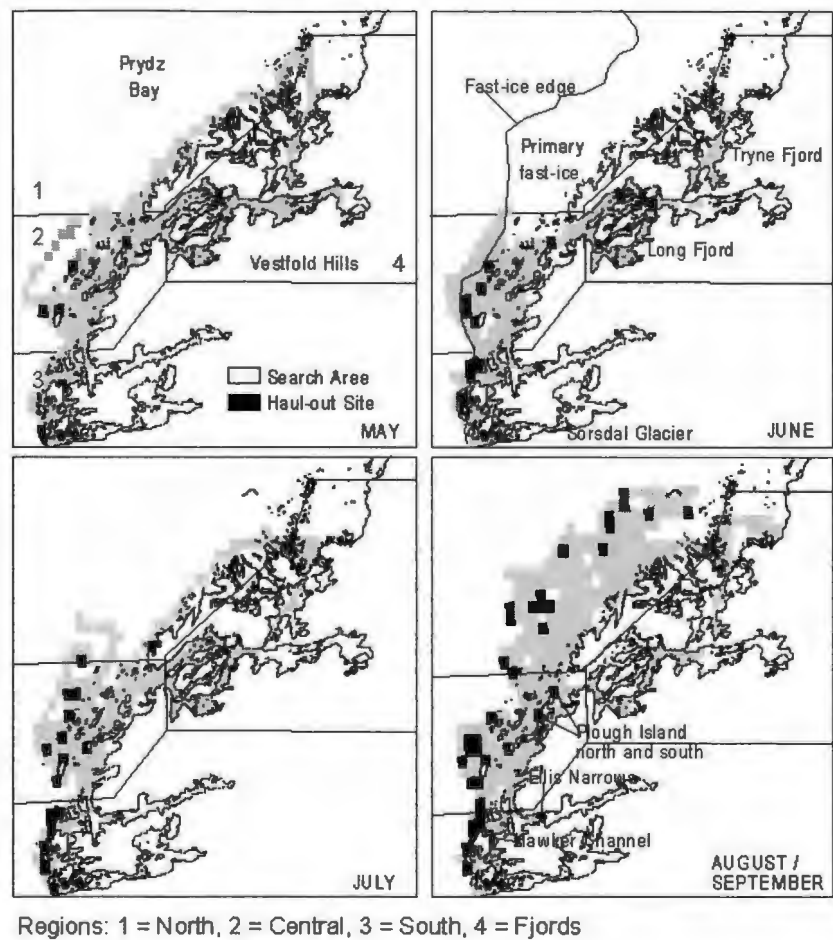


Figure 3-2 Search area and location of haul out sites encountered each month / 2 month period. Search area was defined as the presence of vehicle track locations per gridsquare. The regions numbered are defined in the text.

*Data format, grid-map resolution and extent.*

For modeling procedures, the dataset was limited to August and September so as to control for temporal variation in the distribution of seals. The data were reduced to presence or absence of haul out sites per grid square. The grid squares were 0.65 km<sup>2</sup> to take into account the resolution of the GPS. The grid map's point of origin was 68°20'S, 77°48'E, with 45 rows and 47 columns. The grid was reduced to ocean areas only using GIS (Geographical Information Systems) software (Arcview GIS 3.1). Some of the derived cells were less than standard size possibly affecting the likelihood of being surveyed. Therefore grid area was included in the models as a correction variable.

The spatial extent of coverage was limited according to intensity of search effort. An index for search effort was interpolated so as to account for the zigzag movement of the tracked vehicle, as well as the second vehicle working in line of sight of the tracked vehicle. The index was interpolated by

creating a layer of 50 m<sup>2</sup> raster cells, the value of each raster being the distance to closest vehicle point location. The index of search effort was the average value of raster cells per grid square. Univariate correlation showed that all seal sightings occurred in cells with index of search effort <500 m. Thus analysis extent was limited to grid cells with values of search effort from 0-500 m.

### *Spatial analyses and MAUP*

The results of modeling were likely to change according to the shape and size of analysis extent. This is known as the moveable area unit problem (MAUP) (Svancara et al. 2002). If the study area was homogeneous then the process of aggregating the data would have had a smoothing effect. However, it was ascertained by direct observation that the Vestfold Hills was not an homogenous habitat for Weddell seals. There were fjords, where sea ice was relatively close to land. There was the area adjacent to the Sörsdal Glacier, where the fast ice edge adjoined a narrow chain of islands. There was an area adjacent to the central coast with coastal islands and ice bergs further offshore, retaining a tract of fast ice of medium extent (3-4 km). There was also an area adjoining the northern coast with ice bergs retaining a tract of fast ice of several kilometers wide (6 km). Given this heterogeneity, results of modeling would depend on the area of data coverage. Thus these 4 regions of relatively homogenous habitat were defined. The models were run using subsets of regions rather than each region separately. This was to increase the number of sampling units and thus correlative power of the models. Subsets of the regions were; all regions; northern region only; southern regions i.e. south, central and fjords, and offshore regions i.e. north, south and central (Figure 3-2).

### *Environmental parameters*

The environmental variables quantified for modeling included distance to land (mainland and islands), distance to coast (mainland only), distance to ice edge, distance to ice bergs, and number of ice bergs per grid cell. Most of the environmental variables were interpolated in GIS by distance calculations in the same way that the index of search effort was created. Spatial coverages for both land and coast were specific to the Vestfold Hills and obtained from the Australian Antarctic Division data centre (<http://www.aad.gov.au>). Locations of ice bergs were digitised from a Landsat 7 satellite image acquired the summer after survey (30 January 2000, Path 126, Row 108, ground resolution 200 m). Both distance to, and number of, ice bergs per grid cell were calculated from the digitised layer. Location of ice edge was determined from 30 waypoints collected between July and September, and interpolated by copying the shape of the ice edge from NOAA-AVHRR (National Oceanic and Atmospheric Administration - Advanced Very High Resolution Radiometer) satellite images (ground

resolution 1.1 km). The “ice edge” was defined as the edge of the sheet of fast ice that was retained throughout winter (Figure 3-1). The shape and location of the ice edge did change by ca 1 km from August to September in 1999, particularly in the central and northern areas.

#### *Modeling procedures*

Resource selection functions were developed by generalised additive models (GAM's) (Hastie and Tibshirani 1990) which are an alternative to linear regression models that consider log and non-parametric relationships as well as linear functions in model selection procedures. GAM's are an extension of the standard generalized linear model (GLM), which in turn is an extension of the standard regression model. GLM's assume: 1) the response  $y$  may be distributed about its expected value  $\mu$  according to any distribution  $F$  from the exponential family (including the normal, binomial, and Poisson distributions),

$$y_i \sim F(\mu_i),$$

2) the predictors  $x_1, x_2, \dots, x_m$  enter the model through the linear predictor  $\eta$ , which is related to the expected response  $\mu$  by a monotonic function  $\eta_i = \eta(\mu_i)$  called the link function,

$$\eta(\mu_i) = \eta_i = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \dots + \beta_m x_{mi}.$$

These features relax the restrictions imposed by the standard regression model on both the distribution of the response, and the functional relation between the response and predictors.

For presence absence data,  $F$  is the binomial distribution, and the canonical link is the logit transformation, so the full model takes the form

$$y_i \sim \text{Bin}(1, \mu_i)$$

where

$$\log[\mu_i/(1 - \mu_i)] = \eta(\mu_i) = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \dots + \beta_m x_{mi}.$$

GAM's extend GLM's by assuming the linear predictor is of the form

$$\eta(\mu_i) = \eta_i = f_1(x_{1i}) + f_2(x_{2i}) + \dots + f_n(x_{ni})$$

where  $f_i$  are arbitrary smooth functions that are to be estimated (Hastie and Tibshirani 1990). That is, where a GLM estimates regression coefficients  $\beta_0, \beta_1, \dots, \beta_m$ , a GAM estimates smooth functions  $f_1, f_2, \dots, f_m$ , and where the results of a GLM are typically presented as tables of coefficients, the results of a GAM are presented as plots of the estimated  $f_1, f_2, \dots, f_m$ . There is no requirement that all the  $f_i$  are to be estimated - it is possible for the functional form of some of the  $f_i$  to be specified apriori. When

every  $f_i$  is specified, the model reverts to a GLM.

The level of smoothing imposed on the estimated  $f_i$  is arbitrary and controlled by a number of smoothing parameters. These parameters are in essence arbitrary but typically chosen according to a data-driven automatic selection rule (Simonoff 1996). The great advantage of GAM's is that they automatically transform each predictor to give the best model fit, relieving the user of the burden of selecting the form in which predictor variables should enter the model. Although GAM's provide great flexibility, their key disadvantage is that they are purely additive - it is not possible in standard GAM's to represent arbitrary interactions amongst predictors. However, some limited modelling of interaction is possible through the use of bivariate smoothers (Wood 2003).

In a GLM, inference is based on the theory of maximum likelihood estimation - likelihood ratio tests and analysis of deviance replace the classical F-tests and analysis of variance of the standard regression model (McCullagh and Nelder 1989). Inference for the GAM is also based on the theory of maximum likelihood estimation, but is conditional on the choice of smoothing parameters. That is, test p-values account for the uncertainty due to the distribution of the response about its expected value, but do not account for uncertainty in the choice of smoothing parameters. For this reason, test p-values (such as Wald's statistic) should only be taken as an approximate guide. A useful measure of comparative model fit that forms a natural basis for stepwise model selection procedures is the Akaike Information criterion (AIC). This statistic provides a tradeoff between model fit and model complexity, with smaller values of the AIC being preferred, and comparisons limited to within each dataset (Venables and Ripley 1999).

Standard GAM and GLM models are both predicated on the assumption that responses are independent. Yet for spatially extended data, this is unlikely to be the case (Lindsey 1997). Rather, it is likely that responses will be auto-correlated - that is, adjacent responses are more likely to be similar than distant responses, in this case due to con-specific attraction or the greater chance of seals encountering new openings in the vicinity of existing sites. To concede for interdependence of the response variable the GAM was augmented with a term that accounted for auto-correlation, specifically a count of presences in the 4 adjoining grid squares where haul out sites were present. The term was included in modeling procedures as an adjustment variable, similar to terms for area of grid cell and index of search effort.

There was one more check of the validity of analysis. Variance inflation factors (VIF) quantify the degree to which any one predictor can be replaced by the remaining terms in the model. VIFs >10 are considered to be an indicator of multi-collinearity (Neter et al. 1990). For GLMs, VIFs can be calculated by the method of Davis et al. (1986).

## RESULTS

### *Field observations*

Haul out sites in different regions of the Vestfold Hills were associated with different types of habitat (Table 3-1). In the south, most haul out sites were at the fast ice edge. In central and northern regions, haul out sites were mainly at cracks and ice bergs within the tract of fast ice seaward of land and islands. Furthermore, it was apparent from the temporal series of field observations that, early in winter, there were haul out sites in fjords and island chains, but those froze over and no new sites were encountered in the inshore zone. Offshore, specific sites froze up but new sites were encountered continually throughout the winter such that the number of sites in offshore areas actually increased over time (Table 3-1).

In the southern region, most of the haul out sites were at the permanent fast ice edge (Table 3-1). Transitory (semi-permanent) fast ice was least stable in this region, and a loose, tide crack formed where the transitory fast ice hinged with the permanent fast ice and islands. The seals enlarged this tide crack in places thereby creating holes where they could haul out of the water. They also intermittently used a site within the permanent fast ice in the narrow channel between Hawker Island and the main land, and another where open water formed naturally due to fast moving currents at the entrance to Ellis Fjord (Figure 3-2). However, the lack of scats and imprints at these two inshore sites suggested infrequent use, possibly due to isolation from other holes.

In the central and fjord regions, there seemed to be 2 types of habitats - sites inshore of the islands which were associated with land, and sites offshore of islands which were associated with ice bergs or the ice edge. Of the 10 inshore sites that were encountered, only Plough Island south was created late in winter, and only Plough Island north was maintained over time (Figure 3-2). Notably, these sites were at the entrance to Long Fjord and may have facilitated early arrival to breeding sites. The hole maintained throughout winter developed into a deep tunnel due to ice building up on the ice surface. To keep the hole functional, seals reamed the ice with their teeth. In the fjords, there were 4 haul out sites in May and June. These closed over and there was no evidence of seals hauling out in fjords for the rest of winter (Table 3-1). Offshore of islands in the central region there was a tract of fast ice ca 3 km wide. Different haul out sites were encountered every month. When old holes were revisited they frequently had closed over, yet the number of haul out sites encountered per month increased over time (Table 3-1). Thus it was apparent that new sites were being generated in offshore areas. The majority of these sites were amongst the ice bergs. Only two sites were at the fast ice edge. Similarly, in the northern region, the majority of haul out sites were at ice bergs and cracks rather than the fast ice edge (Table 3-1).

*Modelling the data*

The aim of modelling was to develop resource selection functions. The environmental gradients quantified for analysis were hypothesised to be related to seal distribution on the basis of existing knowledge about the ice and the seals' ecology. Using Generalized Additive Models, the relationships between variables and haul out sites could be smoothed functions of the data or linear or log coefficients. Interpretation was based on the shape of functions, compared and contrasted between subsets of regions, and rationalised using knowledge obtained directly from field observations.

An examination of variance inflation factors (VIF) for the GLM containing all main effects showed minimal evidence of multi-collinearity. The largest VIF was 5.6 for distance to coast. With this term removed, the VIFs for all variables were  $<2$ . Model selection was based entirely on AIC. Models were compared that varied according to initial configuration (linear, log or smoothed function - denoted by "S" in Table 3-2). Furthermore, some models were constrained to include correction terms such as search effort and auto correlation. The strength of findings was in the consistency of variable selection and form (linear or function), within each subset of regions, despite changing the initial model configuration (Table 3-2). The exception was northern region models, which had the least degrees of freedom ( $n = 164$  grid squares). Figure 3-3 shows that the main source of variation in the results was between regions, with the shape of predictor functions changing according to the subset of regions used for modeling. This indicated that MAUP was indeed a concern for parameterising the seals' distribution, and that habitat composition needed to be considered when interpreting results.

Distance to ice edge was included in models for all 4 subsets of regions (Figure 3-3). The strong relationship with seal distribution was confirmed by significant Wald's statistics in both the northern region and the offshore subset (Table 3-2). All functions had probability of encounter increasing with proximity to the fast ice edge. There was a second peak at 3000 m in the northern area model, but similar probability of haul out between 1000 and 3000 m in models for all areas and all offshore areas, possibly because the peak at 3000 m in the northern area was counterbalanced by the linear decrease from the fast ice edge in the model for the southern area. Figure 3-3 shows that, beyond 3000 m, confidence estimates around the trends were increasingly large.

Distance to land was included in models for all analysis extents except the southern area, but the Wald's statistic was only significant for the offshore subset (Table 3-2). Relationships were consistently functions (Figure 3-3). However, the shape of functions differed dramatically between models. In the northern region, there was decreasing occurrence of haul out sites within 3000 m of land, albeit with very wide confidence intervals. For the offshore subset, there was increasing occurrence within 2000 m of land. For all regions collectively there was increasing occurrence within



2000 m of land, dropping sharply within 1000 m of land, reflecting the fact that fjords were unoccupied at that time of year. The difference between functions for northern region, where the fast ice tract was extensive, and the offshore subset, which included many cells where the land was close to the ice edge, indicated that proximity of land to the ice edge changed the seals' relationship with land. It seemed that winter haul out sites were associated with land only if land was near the ice edge.

Table 3-1 Number of haul out sites directly associated with specific features of the sea ice for each region of the Vestfold Hills (see Figure 3-2), and each month of survey. Percentage of monthly total shown in brackets. \* If site at both ice edge and island then categorized as ice edge.

Area	Habitat	May	June	July	August	September	Total
North	Crack	.	.	.	6 (24)	7 (36)	13 (20)
	Iceberg	.	.	.	18 (72)	25 (64)	43 (67)
	Iceedge	.	.	.	1 (4)	4 (10)	5 (8)
	New ice	.	.	.		3 (8)	3 (5)
South	Crack	0	0	1 (5)	0	0	2 (2)
	Iceberg	0	1 (7)	0	1 (3)	0	2 (2)
	Ice edge	0	10 (71)	18 (95)	27 (87)	12 (75)	67 (84)
	Island*	0	3 (21)	0	2 (6)	4 (24)	9 (11)
	New ice	1 (100)	0	0	1 (3)	0	1 (1)
Fjords	Crack	2 (100)	4 (100)	0	0	0	6 (100)
	Iceberg	0	0	0	0	0	0
	Island	0	0	0	0	0	0
Central	Crack	2 (25)	5 (24)	5 (24)	3 (14)	3 (8)	18 (19)
	Iceberg	1 (13)	10 (48)	9 (43)	4 (19)	11 (42)	35 (36)
	Iceedge	0	0	1 (5)	7 (33)	5 (19)	13 (13)
	Island	5 (63)	6 (29)	6 (29)	7 (33)	7 (27)	31 (32)
	New ice	0	0	0	0	0	0

Post inclusion of the above variables, distance to ice bergs was selected for the northern region and the offshore subset (Figure 3-3). Consistent linearity of the term (Table 3-2) indicated that there were more haul out sites in the vicinity of ice bergs. Correction factors for search effort and grid area were also included in most of the models. The auto-correlation term was included in all models. Where the auto-correlation term was deliberately excluded, the difference in AIC confirmed that haul out sites were more likely to occur nearby other sites (Table 3-2).

Maps of the fitted probability of seal presence were generated using predictions from the binomial GAM for offshore regions, both including and excluding the term for auto-correlation (Figure 3-4). For the thresholds, probabilities >0.5 were classed as present, and <0.5 as absent. The difference between plots demonstrated that 1 cluster of 4 points wouldn't have been predicted on the basis of environmental variables, without the auto-correlation term. The models predicted seals to occur

within a broad band in offshore fast ice, yet haul out sites were observed in only some of those cells. The false positives suggest that the offshore area did not become saturated such that there were haul out sites everywhere within that zone. The observed distribution also differed from the model prediction with regard to false negatives where inshore sites were not predicted (Figure 3-4). I know from direct observation that the few inshore sites still open in August and September were old holes maintained over time and thus not related to environmental factors determining the distribution of haul out sites late in winter.

Table 3-2 Terms structure, AIC and Wald tests for the final fitted models. For each predictor, I indicate whether the predictor entered the model as a linear parametric term (Lin) or a smoothed function of the data (S). For reference, asterisks indicate terms significant according to Wald statistic ( $p < 0.05$ ). Variables forced into the model are denoted (1). Auto = autocorrelation, Area = area of grid square, Effort = search effort, Land = distance to land, Coast = distance to coast, Edge = distance to ice edge, Berg = distance to ice bergs, and Nberg = number of ice bergs per grid square. DF = degrees of freedom. See text for definition of subsets of regions.

Model	Auto	Area	Effort	Land	Coast	Edge	Berg	Berg2	AIC	DF
All regions	Lin	Lin	Lin	S		S			236.4	519
North linear	Lin		Lin	S		S*	Lin		96.3	164
“ functions	Lin			S		S*	Lin	Lin	95.6	164
“ linear S.effort <sup>1</sup>	Lin		1	S		S*	Lin		98.2	164
“ function S.effort <sup>1</sup>	Lin		1	S		S*	Lin	S	99.4	164
South linear	Lin	S	S*			S			117.1	294
“ functions	Lin	S	S*			S			116.8	294
Offshore linear auto	Lin		Lin	S		S*	Lin		215.4	315
“ linear not auto <sup>1</sup>	1		Lin	S*		S*	Lin		222.0	315

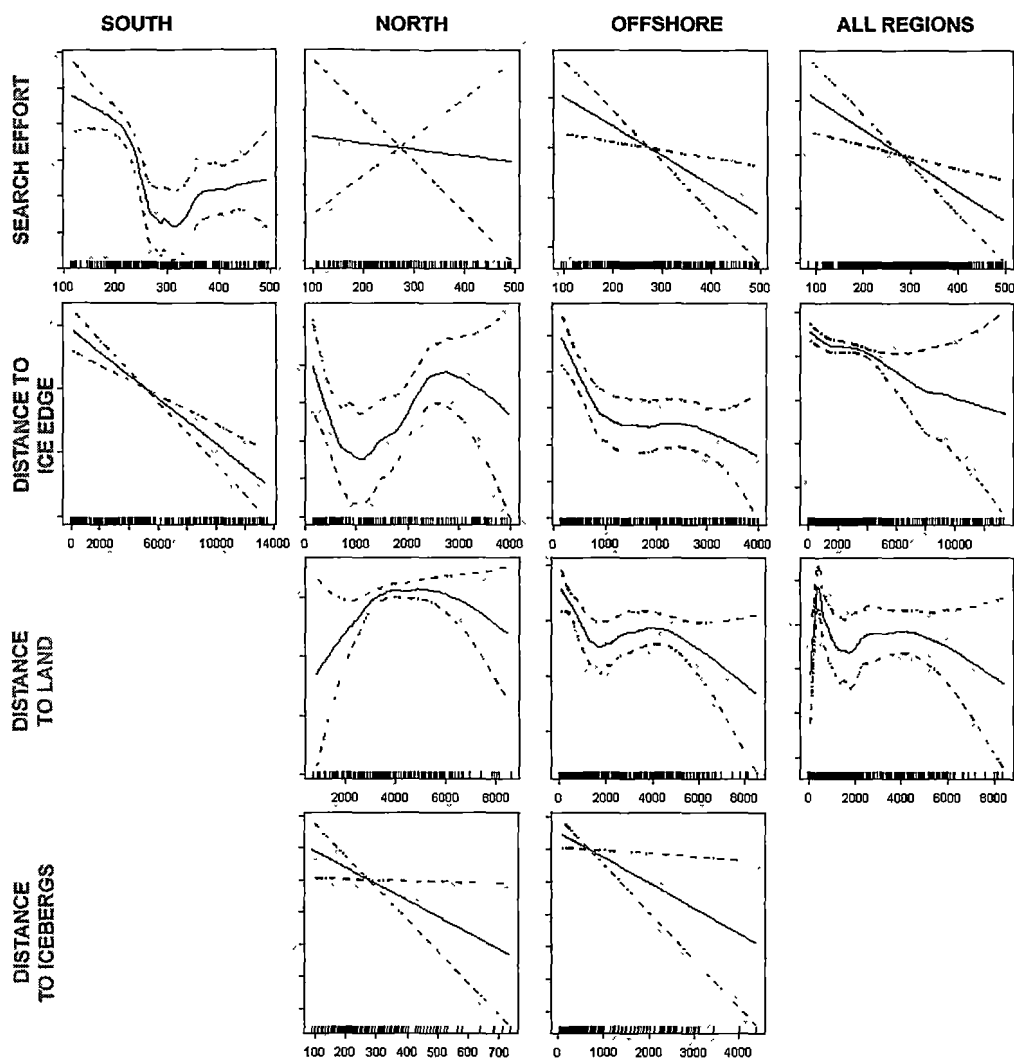


Figure 3-3 Functions of predictors estimated by GAMs for the various sub-sets of regions of the Vestfold Hills (South, north, offshore and all regions). The y-axis of each plot is on the scale of the linear predictor, and dashed lines show approximate 95% confidence intervals.

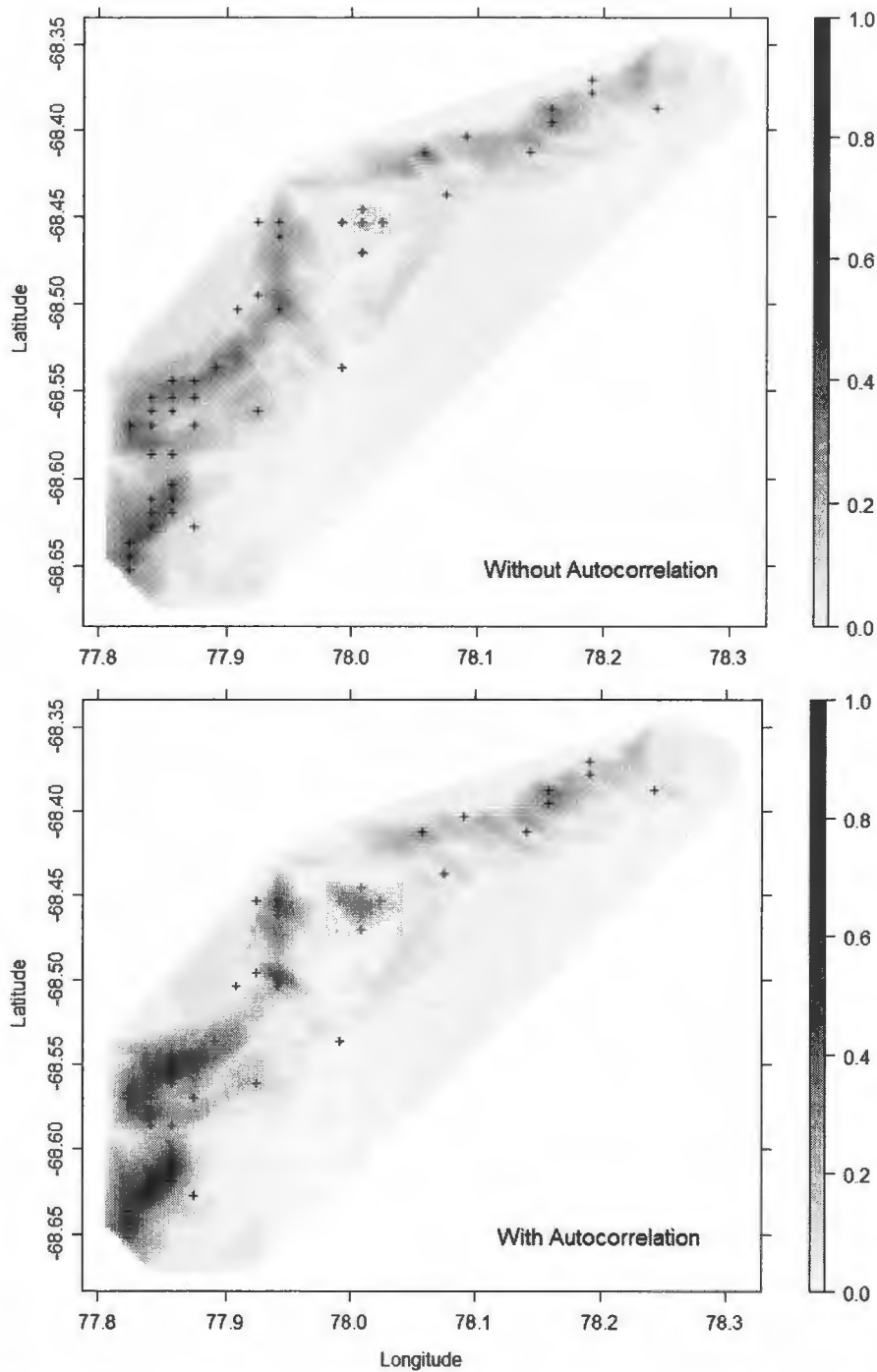


Figure 3-4 Maps of the fitted probability of seal presence as predicted by the binomial GAM, where “+” denotes actual observations of haul out sites. The predictions are from models of the offshore subset (regions 1-3), with and without the term for autocorrelation (see text for definition). The threshold for presence / absence was 0.5 probability.

## DISCUSSION

This is the first quantitative study of Weddell seal distribution in winter. The role of the study, as a ground survey and thus limited in scope, is in providing preliminary data and thereby guiding future surveys. In presence/absence models, it is generally accepted that robust measures of prediction success make use of independent data i.e. data not used to develop the models (Fielding and Bell 1997). However, I chose not to withhold a sub sample for testing because this would have lessened the correlative power and thus accuracy of the models (Fielding and Bell 1997). I chose to use all the data and maximise model performance thereby generating hypotheses for testing by future study. I used GAM's to automatically transform each predictor to give a smoothed function representing the best model fit. The two strongest predictors of seal distribution were modeled using these smoothed functions, rather than linear or log relationships. This demonstrated how, for this analysis, GAM's provided better fitting models, thus better predictions, and more information for interpreting the relationships that could not have been obtained by GLM.

Distance to ice edge was the strongest predictor of haul out site occurrence. The predictor function was shaped such that haul out sites were most likely to occur within 3000 m of the fast ice edge. The seals may have needed to be close to the ice edge if they were commuting between fast ice resting sites and open water foraging grounds, for example. In this case, using haul out sites close to the ice edge would have minimized distance traveled and thus energy expenditure. Alternatively, the seals may have been responding to one or more latent variables co-linear with distance to ice edge, such as bathymetry, exposure to warm ocean currents, fast ice thickness, or susceptibility to environmental forcing, all of which increase the propensity for ice to crack. In that case, seal distribution would have been determined by the presence or absence of cracks in the fast ice providing seals with a place to breathe whilst foraging beneath the ice.

It is highly likely that seals were commuting to open water foraging grounds. The fast ice landscape, especially in the southern region, was such that foraging trips further from the coast would have been possible. The seals hauled out at the permanent fast ice edge in the vicinity of the Sörsdal Glacier (Figure 3-4), where transitory fast ice offshore of the ice edge was very unstable and frequently open water. This raises the question why Weddell seals would forage in dynamic ice but return to fast ice to haul out of the water. Mauritzen et al. (2003) discuss how animals depend on a mixture of spatially segregated habitats to fulfill their requirements. Animals experiencing a trade-off between foraging and risk may divide their time between foraging in risky habitat and resting in safe habitat. Fast ice is relatively safe habitat for Weddell seals during winter because it is more constant than dynamic ice, and thus may be familiar to local seals (Kooyman 1975). The shared use of breathing holes aids in

navigation because seals use acoustic cues of con-specifics to estimate the distance and direction of breathing sites (Wartzok et al. 1992). Furthermore, cooperation maintaining breathing holes minimizes toothwear (Stirling 1969) adding to the reasons why Weddell seals would return from offshore to rest on stable, fast ice substrate.

If the fast ice is relative safe then Weddell seals could forage beneath the ice. Again, the seals' distribution shows that this is highly likely. In the central and northern Vestfold Hills, seals were not hauled out at the ice edge. They were at cracks and ice bergs within the fast ice tract, suggesting that they were foraging beneath the ice as opposed to traveling offshore. Kooyman (1975) used dive recorders to understand the behaviour of Weddell seals foraging beneath the fast ice in winter. The seals experience rigors of keeping breathing holes open and navigating under ice in winter darkness. Kooyman (1975) suggested that seals living beneath fast ice learn a great deal about the ice as it thickens. They learn the location of cracks and breathing holes. They probably know the bottom topography intimately. When they feed their dives are almost directly beneath the breathing holes so that they return to the surface under familiar ice topography. If they choose to move to a new area then they may follow a crack system. Kooyman (1975) also suggested that, within the radius from each breathing hole, prey resources become depleted especially if more than one seal is foraging from the hole. Such intra-specific competition could be the reason for aggressive behaviour between individuals and what prompts seals to make exploratory dives, despite the risk of disorientation, to find new cracks in the ice with associated prey resources. In this way, Weddell seal populations foraging beneath fast ice could optimize the use of prey resources. Testa (1994) used satellite tracking of 26 adult females in the Ross Sea to document the movements of Weddell seals in winter. The study showed a lot of individual variation. Some seals were sedentary with very small home ranges, others moved between fast ice and dynamic ice habitats. A few seals made long journeys of up to 3 months and 1500 km into the Southern Ocean. Therefore, it is totally plausible to suggest that seals at the Vestfold Hills were foraging both beneath fast ice and at offshore foraging grounds, and that their distribution is related to both distribution of cracks in fast ice as well as proximity to the ice edge.

Distance to land was another environmental gradient that refined the predictive capacity of models. However, the functions relating distribution of haul out sites to distance to land varied according to analysis extent. Thus, results seemed ambiguous. However, I propose the different shaped functions reflect different relationships between haul out sites and land at different scales of observation. At the micro-level, haul out sites can be directly associated with land because fast ice tends to fracture where land constrains movement. At the macro-level, haul out sites did not form inshore where the ice was relatively thick and stable because it was rigidly frozen to land (in Long Fjord, for example). The analysis was designed to test both hypotheses by including distance to land and distance to coast as

predictor variables. However, the co-linearity evident for distance to coast indicated that models were unable to disentangle the two effects. It is unlikely that such problems would arise in other areas, for the coastline at the Vestfold Hills is unusually intricate. I conclude that cracks are not likely to form where the fast ice is held rigid to the coast, but, where the ice is moving, cracks will form in direct association with land if it is present. Similarly, cracks in the fast ice will form adjacent to ice bergs in offshore regions, hence the inclusion of the variable for ice bergs in models for the northern and offshore subsets.

Future studies investigating the distribution of Weddell seals in winter could aim to determine the point at which there is sufficient distance from land for fast ice to move freely, whilst still being unrelated to distance from the ice edge. If there is such a zone then it would show that the seals' distribution was being determined by factors causing the fast ice to crack, independent of the proximity to open water. In East Antarctica, the seaward extent of fast ice (45 - 65 km, Fedetov et al. 1998) is generally much greater than at the Vestfold Hills (6 - 10 km). Therefore, it could be relatively simple to elucidate the relationship between Weddell seals and the coast by sampling in other areas. An appropriate survey design would be to run transects across the proposed gradient of distribution (Buckland et al. 1993) which, in this case, would be from coast to ice edge, or as far offshore as logistically possible.

The possibility that location of polynyas might influence the winter distribution of Weddell seals highlights the need for broad scale survey to quantify the effects of variables operating at a regional scale. Potentially relevant factors include 1) the extent of fast ice from the coast, 2) the amount of relatively warm or nutrient rich water in the area, 3) the presence or absence of ice bergs, 4) the presence or absence, shape and size of polynyas, and 5) the distribution of potential competitors such as emperor penguins (*Aptenodytes forsteri*). The winter foraging grounds of emperor penguins are also Antarctic polynya-type habitat (Wienecke and Robertson 1997). If the proposed hypothesis is correct and polynyas are favoured habitat for Weddell seals, then there may be competition between Weddell seals and emperor penguins during winter, since they consume similar species and size of prey (Burns and Kooyman 2001). To conduct broad scale surveys from the ground could be impractical considering this study showed that haul out sites were observed only within 500 m of the vehicles. Aerial survey could be more efficient, providing weather conditions and daylight hours did not jeopardize safety of operations. This study showed that the winter distribution of Weddell seals was most limited in August and September. Longer daylight hours at that time of year make late winter the optimum time for survey.

**SUMMARY**

This study describes the distribution of Weddell seals in winter (May - September 1999) at the Vestfold Hills, in Prydz Bay, East Antarctica. Specifically, the spatial extent of haul out sites in shore-fast sea ice was described. As winter progressed, and the fast ice grew thick (ca 2 m), most of the inshore holes closed over, and the seals' distribution became restricted to ocean areas beyond land and islands. Using observations from the end of winter only, Generalised Additive Models (GAMs) were fitted to generate resource selection functions, which are models that yield values proportional to the probability of use. The models showed that seal distribution was defined mainly by distance to ice edge and distance to land. Distance to ice bergs was also selected for models of some regions. Results were presented as maps of the fitted probability of seal presence, predicted by the binomial GAM for offshore regions, both with and without autocorrelation terms. The maps illustrate the expected distribution encompassing most of the observed distribution. On this basis, it is proposed that propensity for fast ice to crack is the major determinant of Weddell seal distribution in winter. Proximity to open water and dynamic ice habitats could also influence the distribution of haul out sites in fast ice areas. This is the first quantitative study of Weddell seal distribution in winter. Potential for regional variation is discussed.



# Chapter 4

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## **Movements of adult female Weddell seals during the winter months**

Chapter 4 appears to be the equivalent of a post-print version of an article published as: Lake, S, Burton, H and Wotherspoon, S. (2006) Movements of Weddell seals during winter months. *Polar Biology* 29: 270-279. The final publication is available at Springer via <https://doi.org/10.1007/s00300-005-0050-0>

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### INTRODUCTION

Weddell seals *Leptonychotes weddellii* are the most accessible of Antarctic seals. They are the only Antarctic seal species to suckle their pups on land—fast ice, and to use holes in continuous sea ice to haul out and rest on the ice surface (Laws 1981, Siniff 1981). Consequently, Weddell seals have been marked and re-sighted for ca. 30 years in both east and west Antarctica (Green et al. 1995, Cameron and Siniff 2004). Mark and re-sight data is valuable because it enables annual estimates of reproductive rate (Nichols et al. 1994, Lebreton and Pradel 2002). As top predators in marine ecosystems (Plötz et al. 2001, Lake et al. 2003), Weddell seal reproductive rate may be an integrated summary of the state of their environment and a synthesis of change in one of the world's most southern ecosystem (Testa et al. 1991, Boyd 1993, Barbraud and Weimerskirch 2001, Weimerskirch et al. 2003, Ainley et al. 2005). However, to interpret reproductive rate as evidence of the environment, it is necessary to identify extrinsic factors that co-vary with, and potentially determine, maternal condition (Croxall et al. 2002, Hindell et al. 2003). In turn, it is necessary to understand distribution of female Weddell seals to quantify environmental variables over relevant geographical areas.

Satellite tracking is a valuable tool for locating marine mammals and birds at sea (e.g. McConnell et al. 1992, Kerry et al. 1997, Wienecke and Robertson 1997, Trathan et al. 1998, Burns et al. 1999, Boyd et al. 2002, Burns et al. 2004). Weddell seals have been tracked at McMurdo Sound (77°44'S 166°30'W) (Testa 1994, Burns et al. 1999, Stewart et al. 2000). In particular, Testa (1994) tracked adult females using satellite transmitters attached to the lower back. Some adult females were sedentary, while others moved between fast ice and dynamic ice habitats. A few made long journeys of up to 3 months and 1,500 km into the Southern Ocean. At McMurdo Sound, all three tracking studies experienced instrument failure. Testa (1994) tracked adult females from the end of summer, and 9 of 26 transmitters lasted 8–9 months. Burns et al. (1999) tracked pups from the end of summer and 2 of 13 lasted 4 months. Stewart et al. (2000) tracked pups from the end of summer and 2 of 4 lasted 8–9 months. In most cases, it was not known whether it was the seal, the attachment or the instrument that failed. Given the limited success rate at McMurdo Sound, this project was a trial of tracking Weddell seals at the Vestfold Hills.

The Vestfold Hills (68°33'S 78°15'E) is 9°N of McMurdo Sound, and in Prydz Bay as opposed to the Ross Sea. Winter air temperatures are on average 7.8°C warmer at the Vestfold Hills, and characteristics of sea ice are unique to the area (Worby et al. 1998, Heil 2005). Satellite tracking was trailed late in winter when sea ice was in advanced stages of growth and permanent fast ice was ca. 2 m thick (Heil 2005). Thicker ice later in the year limited the distribution of haul out sites for Weddell seals at the Vestfold Hills (Chapter 3). The lower-back attachment position used by Testa (1994) was

replicated so that data from the Vestfold Hills and McMurdo Sound could be compared directly.

## **METHODS**

### *Field methods*

The transmitters were two Telonics ST-10 units (7074 and 7075) powered by 8 'A' size lithium cells in series that transmitted every 45 s, and one Telonics ST-6 unit (23453) powered by 4 'A' cells in series that transmitted every 90 s. (Note: because the batteries were in series, the transmission time was limited by the weakest single battery. The 4 battery series produced 6 V while the 8 battery series produced 12 V, but any differences would be related to electronic power demands and not to the number of batteries per se). All three units had saltwater switches that were set to transmit in air. The criteria for selection was the first three females of adult body size encountered on Vestfold Hills fast ice, that were also encountered in spring the previous year, around the time of mating, and thus could have been pregnant. Searches began in May, when ice was suitable for travel, and seals that met criteria were found in June.

The first deployment was the ST-6 transmitter (23453) on 9 June 1999 at the fast ice edge in the southern Vestfold Hills (Figure 4-1). This seal (23453) was flipper tagged as an adult suckling a pup in Long Fjord 1996, and thus was unknown age but she appeared quite old (scarred and grey). The second deployment was the ST-10 (7074) on 11 June 1999 in Long Fjord. This seal (7074) was tagged as a pup in Long Fjord in 1993 and thus 6 years old the following spring. The last deployment was the ST-10 (7075) on 16 June 1999 in central offshore region of the Vestfold Hills. Seal (7075) was tagged as a pup in Long Fjord in 1995 thus 4 years old the following spring. Average age of first pupping is ca. 7 years old (Testa et al. 1990, Chapter 7). Thus, while seals 7074 and 7075 met criteria of adult size, it's unlikely they were mature.

To deploy transmitters, the seals were restrained physically, first with a pole net then on a restraint board (80 x 240 cm<sup>2</sup> marine ply with Velcro<sup>TM</sup> straps), using a head-bag to put them in darkness. Transmitters were attached to the dorsal surface between the hips. The hair was cleaned with acetone, and a layer of pre-heated 2-part epoxy resin (Araldite K268<sup>TM</sup>) was applied to the hair. Transmitters were placed on the resin, fibreglass cloth draped over the transmitter and onto resin 6–7 cm either side, then another layer of resin applied over the cloth to make a thick (2–3 cm), solid attachment. The glue cured despite -30°C ambient temperatures using heat fanned over the attachment area. Transmitters were retrieved in December by locating the seals, restraining them with a head bag (Stirling 1966) and cutting the hair beneath the attachment.

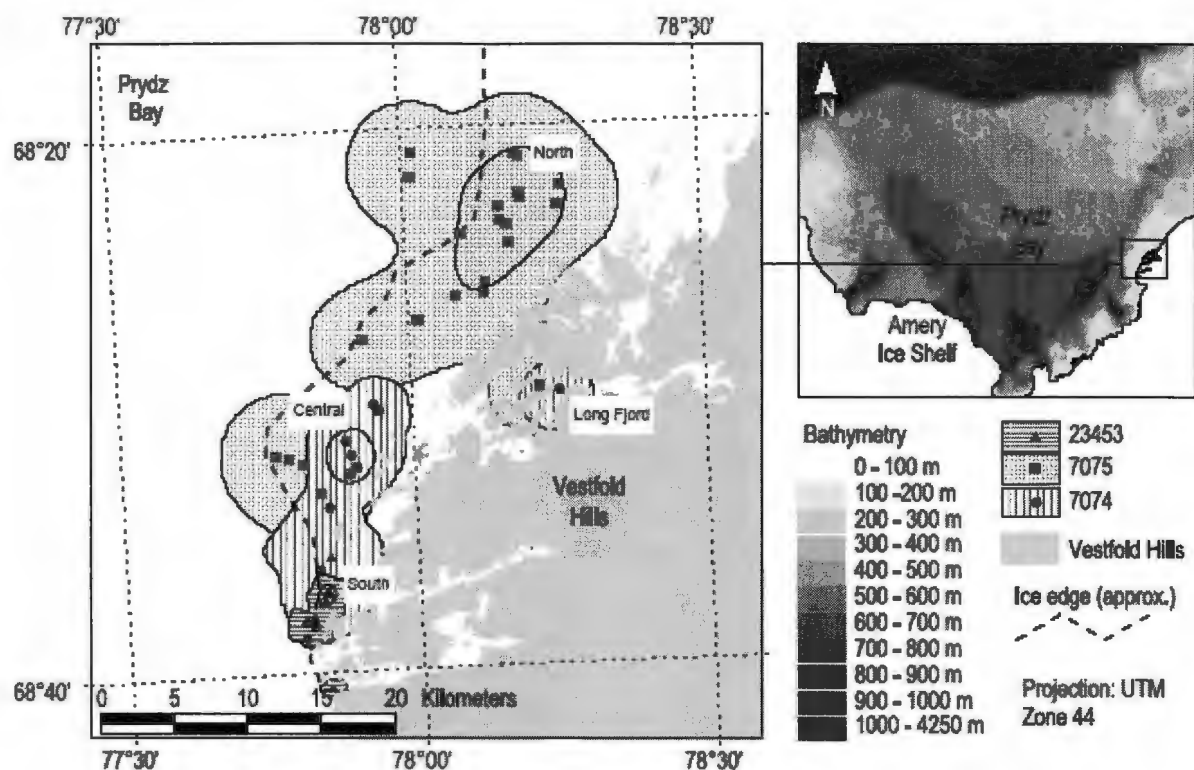


Figure 4-1 The Vestfold Hills, Prydz Bay, Antarctica, showing the relative spatial extents of each seals' home-range, the estimated location of their haul out sites within these areas, regions of the Vestfold Hills as mentioned in the text, and the bathymetry of Prydz bay.

The seals' positions were determined by the ARGOS system (<http://www.argos.com>). To validate precision of ARGOS data, the two ST-10 units were positioned side by side on the ground post-retrieval and allowed 3 weeks to transmit. The actual location of transmitters was determined by differentially correcting position estimates derived simultaneously from two Garmin 12 x 1 GPS (Global Positioning Systems). The precision of ARGOS data was calculated as the standard deviation of the difference between GPS and ARGOS locations i.e. radius in which 68% of locations occurred.

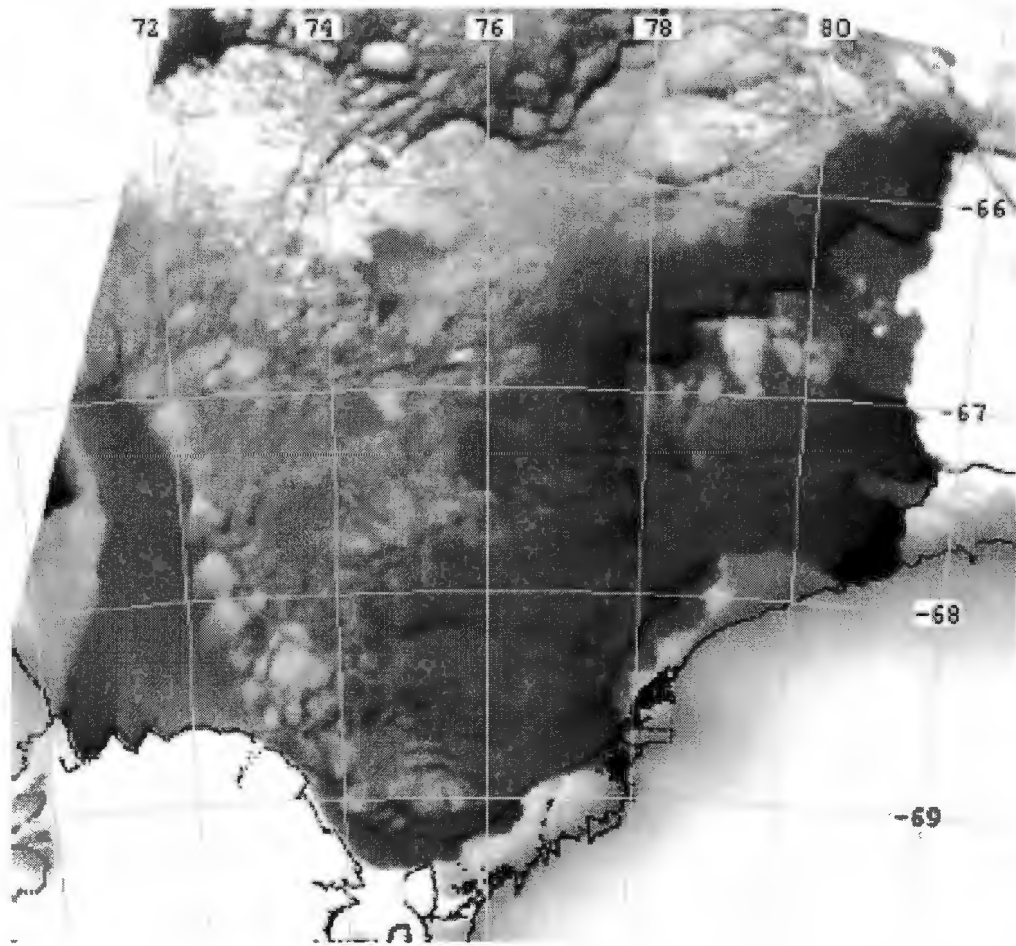


Figure 4-2 NOAA-AVHRR (National Oceanic and Atmospheric Administration/Advanced Very High Resolution Radiometer) satellite image of sea ice in Prydz Bay, showing approximate line of coast and ice-shelves, permanent fast ice (*continuous white*) associated with the Vestfold Hills (68°33' S 78° 15 E, note Long Fjord protruding east and the Sorsdal Glacier between the Vestfold Hills and the islands further south), semi-permanent fast ice (*continuous grey*) attached to permanent fast ice, and dynamic ice further offshore in Prydz Bay (ground resolution 1.1 km)

Hand-held GPS were used to locate the seals on the fast ice and describe their habitat whilst checking the instruments and attachments. On these surveys, the location of the ice edge was ascertained with respect to the seal, and the presence or absence of transitory (semi-permanent) fast ice further offshore was noted, thereby cross-referencing observations of sea ice from NOAA-AVHRR images (National Oceanic and Atmospheric Administration/ Advanced Very High Resolution Radiometer, ground resolution 1.1 km, (Michael and Hill, 2002) Figure 4-2). Haul out sites were visited infrequently so as to minimise disturbance to the tracked seals.

Auxiliary location processing was obtained so that there were 6 qualities of data (i.e. ARGOS categories B, A, 0, 1, 2 and 3). Categories varied in that B, A, and 0 were calculated from three or less satellite fixes and thus were less reliable than categories 1, 2 and 3 which were estimated from 4 or more good location messages (Tailade 1993). Categories 1–3 were included for home range and distance-weighted analyses. Categories 2 and 3 were included for manual analysis. All data were retained for temporal analyses.

### *Data analyses*

Kenward (1993) categorised the parameters of telemetry as home range (size, shape and structure); habitat composition (aspects of habitat within the home range); and movement (distance, headings and speed). Standard movement analyses were not appropriate for tracking haul out sites. Instead the analyses were tailored to show the sequence and use of discrete holes in continuous ice cover (i.e. fast ice). Home range was quantified using kernel density estimation techniques and results were plotted as contour maps, where the contours quantified the distribution of a certain proportion of fixes. Kernel density methods (Silverman 1981) estimate the probability of observing an individual in a given location. Time was not a parameter. In essence, the method “blurred” the set of observed fixes to produce a smooth surface describing the density of fixes across the map. Kernels were calculated in Arcview GIS 3.2 from the Animal movement extension ([www.absc.usgs.gov/giba/gistools.htm](http://www.absc.usgs.gov/giba/gistools.htm)). The least-squares method was used to select smoothing parameters. Nominated home range was 95%, and core area 50%.

Habitat composition was determined in GIS, by plotting the seals’ position fixes with regard to location of the fast ice edge. The ice edge was spatially referenced using 30 waypoints collected between July and September. The shape was interpolated from NOAA–AVHRR images captured over the same period (e.g. Figure 4-2). Ice edge was defined as the edge of the sheet of fast ice retained throughout winter. Shape and location of the ice edge did change by ca. 1 km from August to September in 1999, particularly in the central and northern areas. Most of the seals’ locations were within the area of permanent fast ice. The two exceptions were on continuous ice cover that was advanced semi-permanent and attached to permanent fast ice. Knowing the seals behaviour in fast ice, it was assumed that position fixes were immediately adjacent to the hole through which they hauled out onto the ice surface.

Movement analyses were by distance weighting and manual categorization of position fixes to show sequential use of haul out sites. Both methods relied on the fact that if the seal occupied the same site for a period of time then the degree to which subsequent fixes were similar became exaggerated in the

data. For distance-weighted tracks, each pair of successive position fixes was plotted as a circle at the midpoint of the two fixes, with the radius of the circle proportional to the distance between successive hits. Many small circles close together indicated sites where a seal lingered. The manual method involved viewing the data in sequence in GIS and grouping the data into sets of fixes that occurred sequentially and at approximately the same location. More than one step in the time series was considered simultaneously thereby validating sets of fixes defined on the basis of distance weighting. The location of each site was estimated as the average latitude and longitude of each set of position fixes, with 95% confidence intervals. "Tracks" were drawn between sites to show sequence of use. Number of days at each site was quantified.

Calculations of rates of haul out were independent of spatial distribution and movement. Changes over time were quantified by the number of position fixes per day, and number of consecutive days with or without position fixes. At the latitude of this study (68°S) there were ca. 20 possible data collections per day, once per hour with a gap of about 4 h around solar noon.

## **RESULTS**

Spatial precision of the ARGOS data was estimated to be 987 m latitude and 1,372 m longitude for quality 1 (n=159); 348 m latitude and 577 m longitude for quality 2 (n=266); and 101 m latitude and 137 m longitude for quality 3 (n=270). These estimates were similar to ARGOS estimates of 1,000, 350 and 150 m for qualities 1–3 respectively ([www.argosinc.com](http://www.argosinc.com)). For seals 23453, 7074 and 7075 respectively, the duration of tracking was 170, 175 and 180 days, and 283, 220, 510 position fixes were obtained, of which 123, 72, and 255 positions were qualities 2 or 3. The difference in transmission rates (45 s or 90 s) did not change the likelihood of obtaining position fixes at sea, since all position fixes were from fast ice. None of the tracked seals gave birth the following breeding season.

### *Spatial analyses*

Seal 23453 (parous adult) hauled out only at the fast ice edge in the southern Vestfold Hills (Figure 4-3). Semi-permanent fast ice offshore of the ice edge was very unstable in this area. She used the loose crack that was the hinge between the fast ice and semi-permanent ice. Or, when the semi-permanent ice had blown away, she accessed the fast ice directly from open water. This seal had the smallest home range (14 km<sup>2</sup>). Her core area of haul out sites was only 1 km<sup>2</sup> for the whole 6-month period. She used ca. nine holes (Table 4-1) although it was difficult to define individual sites and this resulted in large confidence intervals around the estimated locations of her haul out sites (Table 4-1).

Seal 7074 (6 years old) was one of the last three seals hauling out in Long Fjord that winter. Post-deployment, she hauled out infrequently (Figure 4-4). When she did, it was in central and then southern areas of the Vestfold Hills (Figure 4-3), in the vicinity of open water. This seal's home range and core area were also relatively small (130 and 10 km<sup>2</sup>, respectively). She used eight haul out sites during the 6- month tracking period (Table 4-1).

Seal 7075 (4 years old) moved immediately post-deployment from the central islands to the northern icebergs (Figure 4-3) where satellite pictures (e.g. Figure 4-2) showed that the tract of fast ice was most extensive. She hauled out in the northern fast ice in June, July, August and September. During October and November she oscillated between central and northern areas, before moving into Long Fjord at the end of November (Table 4-1), possibly for mating. This seal had the largest home range (300 km<sup>2</sup>) and core area (36 km<sup>2</sup>), consisting of three discrete areas (north, central and Long Fjord, Figure 4-3). The sequence of use showed that this seal zigzagged between haul out sites, using a relatively large number of sites ( $n = 24$ ).



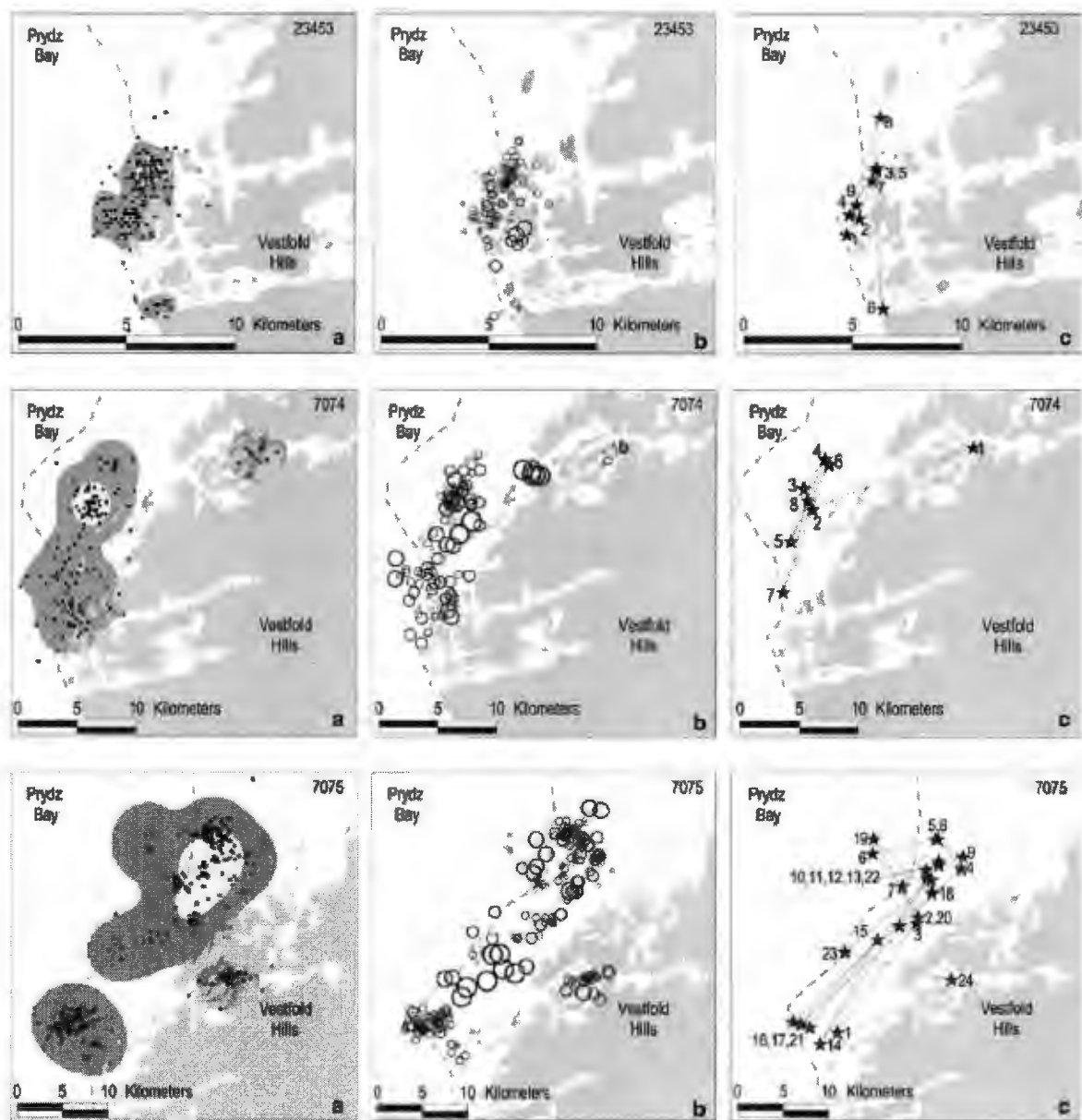


Figure 4-3 Spatial analysis of data from each seal (23453, 7074 and 7075), including **a)** home range as estimated by kernel density analysis, showing 95% (home range) and 50% (core area) contours of density distribution as well as each position fix (qualities 1-3) **b)** movement analysis as depicted by distance weighting where mean location of preceding and subsequent fixes are plotted as a *circle*, and radius of each circle is directly proportional to the average distance between those fixes, and **c)** estimated locations of haul out sites, calculated by averaging sequential position fixes that occurred at approximately the same location. *Numbers* show the temporal sequence of use.

Table 4-4 Estimated location of each seal’s haul out sites (Lat and Long), with 95% confidence intervals (CI), group number for each site (re: Figure 4-3), number of satellite fixes at the site (data quality >1), and the period over which the seal used the site (number of days and dates).

Seal	Lat	ci	Long	ci	Group	Fixes	Days	First and last dates
23453	68.641	0.004	77.811	0.008	1	6	1	16-June
	68.635	0.002	77.827	0.003	2	16	17	21 June-7 July
	68.616	0.003	77.848	0.004	3	22	24	16 July - 8 August
	68.633	0.001	77.816	0.006	4	30	18	10-27 August
	68.614	0.001	77.849	0.003	5	30	21	4-24 August
	68.673	0.002	77.849	0.008	6	10	3	2-4 October
	68.620	0.001	77.844	0.007	7	4	2	22-23 October
	68.593	0.000	77.857	0.000	8	1	1	28-October
	68.629	0.009	77.825	0.029	9	4	6	3-8 November
Total						123	93	
7074	68.500	0.004	78.243	0.009	1	8	4	19-22 June
	68.540	0.002	77.906	0.009	2	5	2	22-23 June
	68.524	0.003	77.890	0.010	3	6	7	13-19 June
	68.503	0.001	77.938	0.013	4	3	2	28-29 June
	68.563	0.000	77.858	0.000	5	1	1	18-September
	68.507	0.003	77.945	0.002	6	4	1	21-September
	68.601	0.007	77.837	0.009	7	22	27	22 Sept-18 November
	68.533	0.002	77.897	0.006	8	23	18	19 Nov - 6 December
Total						72	62	
7075	68.438	0.001	78.124	0.004	2	14	2	20-21 June
	68.440	0.007	78.078	0.008	3	2	1	26-June
	68.388	0.013	78.250	0.022	4	7	2	1-2 July
	68.357	0.002	78.191	0.008	5	38	12	6-17 July
	68.368	0.003	78.013	0.006	6	4	2	24-25 July
	68.403	0.002	78.090	0.004	7	21	5	30 July-3 August
	68.356	0.004	78.184	0.010	8	25	16	6-21 August
	68.376	0.003	78.255	0.014	9	7	2	30-31 August
	68.379	0.001	78.189	0.004	10	3	1	1-September
	68.387	0.001	78.155	0.007	11	3	1	4-September
	68.383	0.001	78.190	0.008	12	4	2	6-7 September
	68.396	0.001	78.156	0.004	13	9	1	10-September
	68.556	0.001	77.845	0.013	14	6	2	17-18 September
	68.453	0.005	78.016	0.017	15	3	3	21-22 September
	68.538	0.002	77.818	0.009	16	8	9	9-17 September
	68.531	0.002	77.772	0.009	17	47	28	18 Oct-14 November
	68.409	0.005	78.169	0.029	18	3	1	15-November
	68.353	0.000	78.018	0.018	19	2	2	15-16 November
	68.433	0.001	78.128	0.004	20	4	2	16-17 November
	68.534	0.005	77.793	0.014	21	5	2	19-20 November
	68.398	0.002	78.168	0.002	22	2	1	22-November
	68.464	0.006	77.924	0.008	23	4	1	24-November
	68.497	0.001	78.210	0.006	24	31	11	26 Nov-6 December
Total						252	109	

*Temporal analyses*

Seal 7075 spent more time hauled out than the other two seals (Figure 4-4). She was recorded on 50% of days (87 of 175 days), compared to only 21 and 25% of days for seals 7074 and 23453 respectively. Furthermore, seal 7075 hauled out more regularly and in longer bouts (consecutive days with position fixes; average duration  $2.7 \pm 1.4$  days) compared with the other two seals ( $1.4 \pm 0.6$  and  $1.8 \pm 0.7$  days, ANOVA  $f_{2,73} = 11.46$ ,  $P < 0.001$ ). The other two seals had periods up to a month without being located (Figure 4-4).

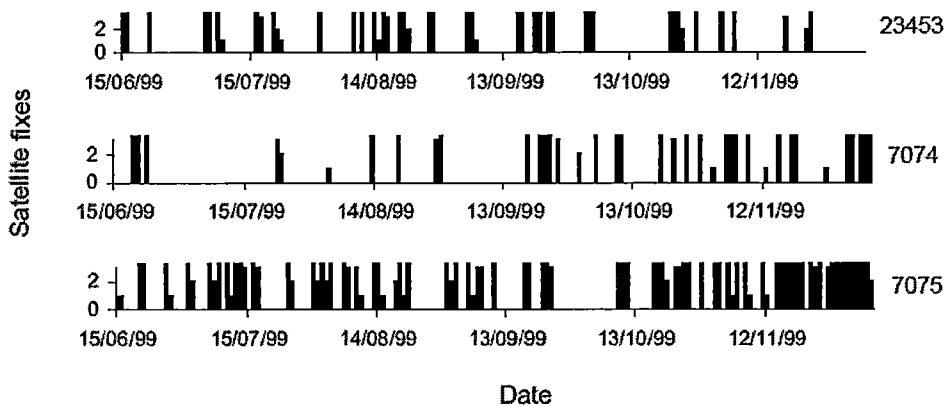


Figure 4-4 Temporal pattern in haul out behaviour for each of the tracked seals (23453, 7074 and 7075), where days with location data (bars showing 1, 2, or 3+ satellite fixes per day) indicate resting periods on top of the ice. Date (day/month/year).

**DISCUSSION**

The aims of this study were twofold: (1) to track adult females in winter without compromising the performance of the instruments, and (2) to describe the geographical range of tracked individuals. The first aim was achieved in that all three instruments functioned for ca. 6 months and then were retrieved. Tracking was from midwinter to the end of the breeding season (October–November). The second aim was not achieved because, as discussed below, two of the three seals had potential to forage further than evidenced by location data.

It was inferred two of the three seals foraged offshore by considering sea ice structure, and also the intervals between haul out activity. Seal 23453 had the potential to forage offshore since she hauled out relatively infrequently and always used sites at the southern ice edge, adjacent to open water or newly frozen ice. Similarly, seal 7074 hauled out infrequently and used sites that were accessible from the southern ice edge, given that Weddell seals can swim several kilometres between breathing sites

(Kooyman 1975). By contrast, seal 7075 had limited capacity to come and go from offshore habitats, since she hauled out regularly (every few days), and used fast ice in the northern Vestfold Hills, where semi-permanent fast ice was relatively wide, thick and stable (Figure 4-2), and could have been a barrier to travel. Kooyman (1975) proposed that when seals forage beneath fast ice in the dark and freezing conditions that are Antarctica in winter, prey stocks become depleted within the accessible radius of each breathing site, which prompts seals to make exploratory dives, despite the risk of disorientation, to find new holes with associated prey resources. As seal 7075 returned to haul out sites, she must have been sharing holes otherwise she could not have left and returned later because the hole would have frozen over. Her reasons for moving regularly between haul out sites could have been social and related to competition for food. Seals 23453 and 7074 used fewer sites (8 and 9 vs. 24 haul out sites, Table 4-1) in smaller areas (Figure 4-1), which supports the theory that they used haul out areas mainly for resting.

If seals 23453 and 7074 did forage offshore, then they did not haul out there, at least not for long enough to fix their position. (The 1–4 h intervals between satellite passes made it possible that short haul out bouts went undetected). When the seals were offshore they could have foraged in the coastal polynya (Worby et al. 1998) or beneath dynamic ice (Figure 4-2) but returned to fast ice as their preferred resting substrate. The hypothesis that Weddell seals prefer to rest on fast ice is supported by relatively few sightings of Weddell seals in shipboard surveys of dynamic ice (Erickson et al. 1983, Bester et al. 1995, Bester and Odendaal 2000, Bester et al. 2002, van Dam and Kooyman 2004). Similarly, southern elephant seals (*Mirounga leonina*) are rarely seen in shipboard surveys but are known to inhabit dynamic ice covered ocean (McConnell et al. 1992, Hindell et al. 1999, Field et al. 2001). These Weddell seals may have divided time between foraging in risky habitat and resting in safe (retreat) habitat, similar to polar bears (*Ursus maritimus*) in the Arctic (Mauritzen et al. 2003). Polar bears use highly dynamic ice near the stable ice edge for hunting. However, they risk drifting away in dynamic ice—thus they retreat to more stable ice for resting. In this study, all three seals faithfully hauled out in areas of fast ice. Burns et al. (1999) showed that Weddell seal pups also had periods of fairly localized movement. Kooyman (1975) suggested that Weddell seals use discrete areas of fast ice so that they can rely on spatial memory, and perhaps acoustic cues of con-specifics, to navigate within established breathing networks in dark and freezing conditions. The results of this study clearly demonstrate that adult female Weddell seals are able to find winter retreat in specific areas of land—fast ice as an alternative to migrating north for winter.

If Weddell seals forage and rest in different habitats, then tracking haul out sites will never be good

evidence of foraging range. To gain more complete evidence would require attaching transmitters to the head to obtain position fixes from the water as well as on top of the ice, as used by Burns et al. (2004) for crabeater seals (*Lobodon carcinophagus*). However, during winter Weddell seals in fast ice areas have been observed to use holes only big enough to expose their nose to the air (S. Lake, personal observation). With transmitters on their head, capacity to use small breathing holes would be compromised, undermining networks of breathing sites, winter foraging behaviour and possibly survival. Considering this, instruments would be damaged in the process of seals attempting to breathe. A neck mount might be more appropriate, as used by McConnell et al. (1992) for southern elephant seals. However, a Weddell seals' neck is more dynamic than the lower back, moving and stretching as seals lunge for prey (Sato et al. 2002). Another option is to replicate the lower back attachment and simultaneously use sensors to collect evidence of diving and other movement for more complete evidence of foraging and resting behaviour (McConnell et al. 1992, Burns et al. 1999, Burns et al. 2004, Staniland et al. 2004).

Testa (1994) used lower back mounts to track Weddell seals through dynamic ice at McMurdo Sound. Presumably those adult females hauled out at sea. Similarly, pups tracked from McMurdo Sound hauled out in dynamic ice areas (Burns et al. 1999; Stewart et al. 2000). This study's contrasting result, whereby seals at the Vestfold Hills hauled out only in fast ice, could be due to location-specific factors, like polar bears in the Arctic Archipelago using land-fast ice more intensively than bears in Baffin Bay which used moving ice (Ferguson et al. 2000). However, the difference between studies is currently attributed to larger sample sizes and summer deployment at McMurdo Sound. At McMurdo Sound, the tracked seals dispersed from coastal fast ice prior to winter, and showed marked diversity in individual foraging range. In this study, a small number of seals was sampled from winter fast ice, thus results could be biased toward sedentary individuals. Perhaps seals ranging more widely from the Vestfold Hills did haul out on dynamic ice but this was not sampled. Different foraging ranges would minimise intra-population competition, and maximise the complexity of demographic response to changes over space and time in food availability (Murphy 1995). The potential bias of this, relatively homogenous sample demonstrates the importance of deploying instruments prior to summer dispersal to document the full range of movements of adult females in the population. These instruments were deployed midwinter to test their performance in thick sea ice. There was 100% success with instruments, suggesting that summer deployments could last through winter. However, the summer moult cycle (Green et al. 1995) and shedding of instruments is a potential source of attachment failure, and further trials might be necessary to assess this effect prior to embarking on a large-scale tracking program.

To interpret reproductive performance with regard to changes in the environment it is necessary to ascertain the seals' foraging habitat as well as their geographical range (Croxall 1992, Croxall et al. 2002, Hindell et al. 2003, Macdonald and Rushton 2003). Weddell seals at the Vestfold Hills definitely forage over the continental shelf throughout the year (Green and Burton 1987, Lake et al. 2003). It is necessary to ascertain whether they also forage beyond the shelf break during summer and winter while they are gestating so as to identify the extrinsic factors that determine reproductive rate. (The shelf break is only 80 km from the Vestfold Hills, less than a day's travel, Figure 4-1). At the shelf break, there is warm upwelling oceanic water (Bindoff et al. 2000), which tends to be highly productive and attract much biological activity (Tynan 1999). The Antarctic continental shelf is characterized by negative winter seawater temperatures ( $-1.8^{\circ}\text{C}$ ) and consequently, endemic fish fauna (Eastman 1993, Tynan 1999, Ackley et al. 2003). Temperature sensors deployed on seals (Field et al. 2001) could locate foraging to within or beyond the shelf ecosystem. Similarly, analysis of fish species in scats collected during winter or, more specifically, fatty-acid analysis of females' milk (Staniland and Pond 2005), could locate foraging to ecosystem level. A combination of tracking, sensors and diet study would best reveal foraging range and trophic role of Weddell seals during summer and winter.

### SUMMARY

The focus of this study was the distribution of adult female Weddell seals during winter at the Vestfold Hills. Satellite tracking of Weddell seals had never been done before at this location. Hence, this was a pilot study to evaluate the following methods. We attached satellite transmitters to the lower back, where there was least potential to change the seals' behaviour or to damage instruments on the ice. Location data were obtained only where the seals hauled out, not necessarily where they were feeding. All locations were within the area of fast-ice that was associated with the Vestfold Hills. There were gaps of up to 30 days in the location data sets. Each instrument ( $n=3$ ) remained attached and functioning for ca. 6 months. During that time, two of the three seals hauled out within small areas adjacent to, or nearby, open water. The same seals hauled out sporadically. We inferred that these seals foraged offshore whilst returning to fast-ice to rest. If Weddell seals forage beneath dynamic ice but return to stable ice as their preferred resting substrate, then evidence of haulout sites will always be a biased measure of foraging range. Tracking seals in the water may be possible using alternative placement of transmitters. However, there is potential for instruments to interfere with movement (breathing and prey capture). For this reason, we recommend a combination of sensors, diet and tracking haulout sites to research winter foraging.

# Chapter 5

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## **Annual Reproductive rate of Weddell seals at the Vestfold Hills, Prydz Bay, east Antarctica, 1973-2000**

Chapter 5 appears to be the equivalent of a pre-print version of an article published as: Lake, S, Burton, H, Barker, R and Hindell, M. 2008. Annual reproductive rate of Weddell seals in eastern Antarctica, 1973-2000, Marine ecology progress series, 366, 259-270, Copyright © Inter-Research 2008

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## INTRODUCTION

High levels of natural variability in the Southern Ocean (White and Peterson 1996, Thompson and Solomon 2002, Park et al. 2004, Turner 2004) necessitate continuous or regular observations over long time intervals (years and decades) to characterize human-induced change. Ships cannot provide long-term monitoring, certainly not in sea ice. Specific ocean surface phenomena (e.g. sea ice cover) can be measured by satellite, with additional parameters measured insitu. In this way, new technologies have facilitated scientific understanding of oceanic processes (National Research Council 1994). Still, there are problems with continuity of coverage, harsh environmental conditions, and power sources for instruments, limiting time series data.

Similarly, there are practical difficulties monitoring biota in the Southern Ocean. For this reason, observations of land-based marine predators are extremely valuable. Studies of higher-order predators have potential to signal changes in the marine ecosystem and show the composite effect of physical phenomena. This type of monitoring is logistically simple because, whilst seals and sea birds forage at sea, they reproduce on land or ice, and some populations reproduce nearby research stations. In Antarctica and sub Antarctica, long-time series observations include Weddell seals (*Leptonychotes weddelli*) at Prydz Bay and the Ross Sea; Adelie penguins (*Pygoscelis adeliae*) in the Ross Sea; southern fulmars (*Fulmarus glacialis*), snow petrels (*Pagodroma nivea*) and emperor penguins (*Aptenodytes forsteri*) at Terre Adélie, and southern elephant seals (*Mirounga leonina*) and leopard seals (*Hydrurga leptonyx*) at Macquarie Island (ACE CRC Workshop 2005). In monitoring these isolated populations, it is assumed that elements of their behaviour, reproductive output and health are signs of availability and quality of food (Hindell et al. 2003). Because these are air-breathing predators, sea ice also directly influences foraging success.

Monitoring a predator population could reveal changes over time in demographic rates. These rates are, in themselves, quantitative measures of the status of a species. As part of a suite of parameters from various populations, the same time series may provide 'snap-shots' of the state of the environment. Ultimately, simultaneous interpretation of multiple time series could be the basis of ecosystem models (Constable et al. 2003). However, this approach to investigating the ecosystem is focused on a predator's 'perspective' of its environment (Fraser and Hofmann 2003): Even where access is not limited by sea ice, a linear response to prey abundance is unlikely, since predators may compensate for declining abundance by increasing foraging effort or switching to other species (Hindell et al. 2003). In the Southern Ocean, ascertaining links between predator 'performance' and fluctuations in environment is particularly challenging due to the paucity of information about meso- and local- scale physical phenomena (Constable et al. 2003). Eventually, if sense can be made of predator performance, the 'response' can only be correlated with environmental events and thereby



generate hypotheses of causal mechanisms: It is rare that causal links can be demonstrated.

Nevertheless, there are many examples of Antarctic predator time series that are congruent with large scale physical phenomena (Whitehead et al. 1990, Testa et al. 1991, Lunn et al. 1994, Boyd et al. 1995, Reid and Croxall 2001, Croxall et al. 2002, Fraser and Hofmann 2003, Jenouvrier et al. 2003, Weimerskirch et al. 2003, Beuplet et al. 2005, Forcada et al. 2005, Jenouvrier et al. 2005, Lea et al. 2006). It is common for the signals of reduced productivity to coincide with El Niño events (e.g. Trillmich and Limberger 1985, Le Boeuf and Reiter 1991, Trillmich and Ono 1991): One of the first studies to propose such a link was based on a reproduction time series from Weddell seals (*Leptonychotes weddellii*) (Testa et al. 1991). Decades later, scientists have documented El Niño-Southern Oscillation (ENSO) forcing physical parameters in the Southern Ocean (Kwok and Comiso 2002, Yuan 2004). It is this type of inference, later confirmed by clear and convincing scientific observations, that led Chavez et al. (2003) to conclude that physical regime shifts in the ocean may even best be determined by monitoring marine organisms.

There have been tag and re-sight programs of Weddell seals at both the Vestfold Hills in East Antarctica (Green et al. 1995) and at McMurdo Sound in the Ross Sea (Stirling 1971, Siniff et al. 1977, Testa et al. 1991, Hastings et al. 1999, Cameron and Siniff 2004). It has long been recognized that Weddell seal reproductive rate has the potential to be a sensitive indicator of the foraging conditions (Siniff et al. 1977, Croxall and Hiby 1983, Testa 1987, Testa et al. 1990, Testa et al. 1991, Hastings et al. 1999). However, in the past quantifying reproduction was problematic (Perrin and Donovan 1984). Previous reports used only a simple method of estimating the proportion of females in breeding state, and that was the ratio of parous (sexually mature) females sighted with and without pups. Those studies recognized that estimates could have been biased because females with pups remained on the ice surface near-continually and thus had higher re-sight potential than females in non-breeding state (Testa et al. 1990). Now multi-strata modeling methods (Brownie et al. 1993) can quantify reproductive rate, estimating the proportion of females in breeding and non-breeding state whilst correcting for state-specific re-sight rates of parous females. These models also account for inter-annual variation in re-sight probabilities, and year and state-specific probabilities of surviving between samples (Nichols et al. 1994, Lebreton and Pradel 2002). The probability of breeding is modeled as a function of breeding the previous year. In this context, reproductive rate is the probability of non-breeding animals breeding, and breeding animals breeding again, in consecutive years.

The modeling method is particularly useful because costs of reproduction can be evaluated (Cam and Monnat 2000). Costs include lower probability of surviving, and lower probability of reproducing, the year after nursing a pup (Stearns 1992). Reproductive costs are relevant to interpreting reproductive

rate as an annual index of foraging because decreased probability of breeding in consecutive years could result in autocorrelation within the time series.

This study used model selection procedures to analyse mark and re-sight observations of parous, female Weddell seals collected from 1973-2000 at the Vestfold Hills. The specific aims were to 1) evaluate temporal variation in survival and reproductive rate of parous females, and 2) evaluate survival and fecundity costs of reproduction. The time-series of reproductive rate was tested for correlation with environmental parameters, once again using model selection procedures.

Environmental parameters included ENSO and winter sea-ice cover over Prydz Bay. ENSO was selected as an environmental parameter because Testa et al. (1991) found evidence of ENSO forcing in Weddell seal reproductive rate at McMurdo Sound. Mid-winter sea-ice cover was a more proximate, ecologically relevant process for which data were available. Model results are discussed with regard to life history strategies and the potential for reproductive rate to be a temporally precise indicator of resource limitation.

## METHODS

### *Mark and re-sight methods*

For this study it was a requirement that each parous female have permanent marks or series of marks that were readily identifiable and readable, and that did not alter the long term behaviour of the seal such that their chance of re-capture or survival was different from the norm. Female Weddell seals and their pups were tagged in the webbing of both hind flippers, and searches for tagged animals were made each year from 1973 until 2000 except in 1997 (Table 5-1). Four-wheeled motorbikes were used to search for seals along the coastline of fjords and bays. In many years, helicopters were deployed to locate seals on outer areas of fast ice. Each seal was checked for tags and, if tags were present then records were made of tag colour, tag number, sex, association with pup, and grid-square location (resolution 0.65 km<sup>2</sup>). Field effort (tagging and re sighting seals) did vary from year to year according to personnel and logistics (Green et al. 1995). -

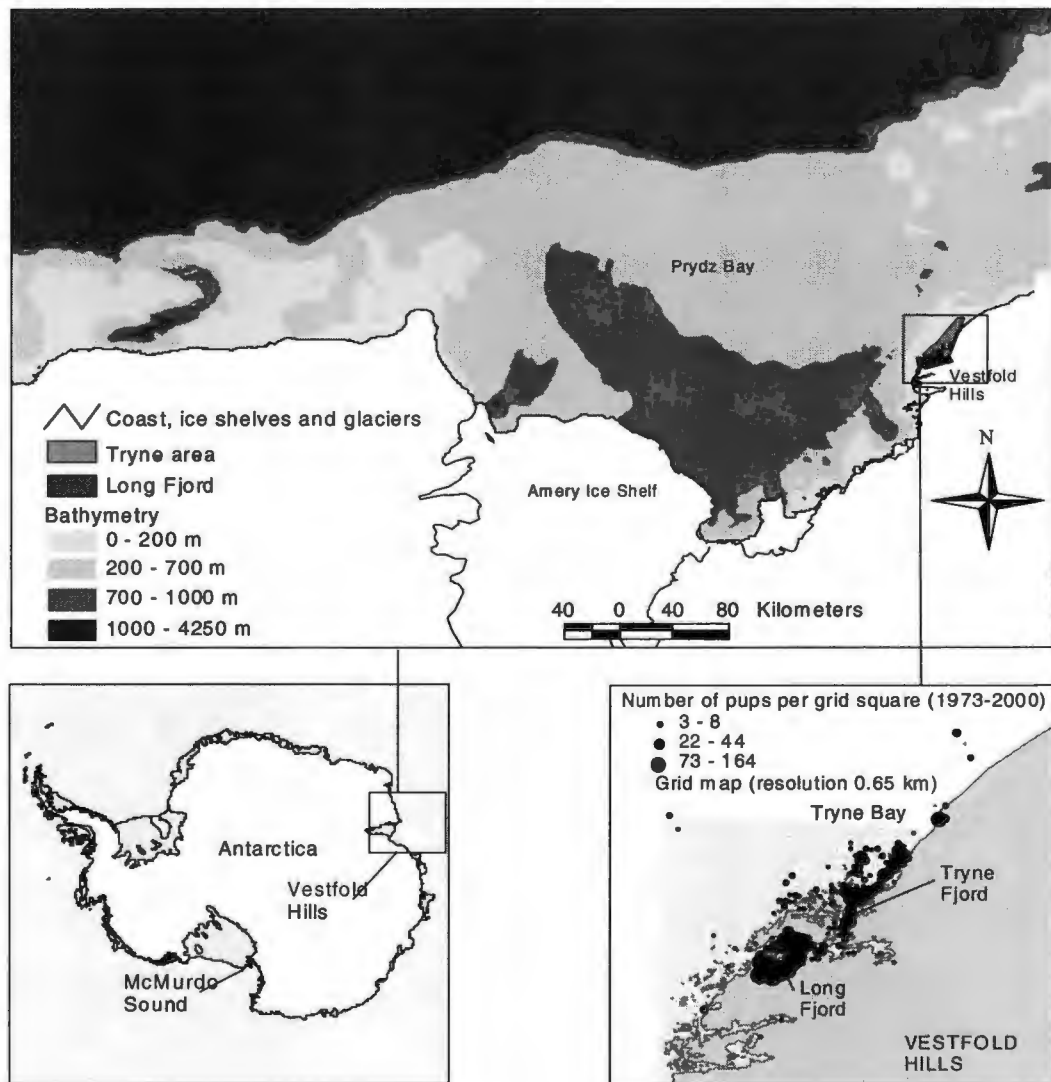


Figure 5-1 Mark and re-sight study areas of Weddell seals at the Vestfold Hills and McMurdo Sound. The Vestfold Hills study area is shown in the context of Prydz Bay. The distribution of breeding sites observed within the mark and re-sight study area are also specified.

The first few years of the program were trials of methods, when adult females were marked with three types of tag. This included aluminum which were small and difficult to read ( $n = 1\,200$  obs), plastic Allflex which were large and had low retention rates ( $n = 600$  obs), and plastic Dalton Jumbo Rototags which were big enough to read and which also had high retention rates ( $n = 20\,900$  obs) (Testa and Rothery 1992, Cameron and Siniff 2004). Dalton Jumbo Rototags were used from 1974 and exclusively from 1980. They were by far the majority of tags deployed. Throughout the program, attempts were made to replace lost tags whilst at the same time minimizing disturbance. Retagging

was done often by ‘surprise’ rather than using physical restraint (Stirling 1966), and a thorough check of the flippers was not made prior to tagging because this would wake the seal and so exacerbate the tagging process. Some animals did eventually have 3 or 4 tags, and not every tag was read at each re-sight occasion because this was not necessary to identify individuals. However, incomplete records of tagging status make it impossible to define the precise date that each tag went missing and in this way calculate rates of tag loss. The report cites apparent rates of survival uncorrected for tag loss. Thus the probability of surviving from year to year could be underestimated, especially in the initial years of the program when tags were newly inserted, seals had fewer tags and various types of tag were being trialed. The probability of loss of single Jumbo Rototags was 0.001 to 0.05 per year (Cameron and Siniff 2004), and the rate of loss may have increased after several years (Testa and Rothery 1992).

Emigration as well as tag loss may account for a seal not being re-sighted even though it was still alive. In this study, models were based on encounter histories of animals in both Long Fjord and the Tryne area (Figure 5-1). Each individual was categorized as a resident of one area or the other, and the difference between areas in rate of emigration was evaluated using model selection procedures. Each individual was categorized as the area in which she bred for the majority of years. The categories were explicit because less than 4% of parous females moved between areas for reproduction (Green et al. 1995, S. Lake unpublished data). Age-specific variation in reproductive rate was controlled by limiting data to parous females i.e. females that had been observed to produce at least one pup, as in Nichols et al. (1994). Most females were marked as adults with pups, rather than as pups, so the sample was representative of all age groups in the breeding population. Lack of surveys in 1997 was incorporated by specifying a 2 year interval.

### *Data analysis*

Multi-strata models use encounter histories of individual seals to quantify the probability of encountering individuals in a given breeding state. Typically mark and re-sight models divide the probability of encountering an individual in terms of: 1) the probability that an animal survived and remained in the study area between samples  $i$  and  $i+1$  ( $\phi$ ), and 2) the probability that the animal was encountered during sample  $i$ , conditional on being alive and in the study area at the time of the sample ( $p$ ). Multi-strata models include a third parameter ( $\psi_i^s$ ), where  $\psi_i^s$  represents the probability that an animal alive and in state  $s$  at time  $i$ , and that survives the interval between samples  $i$  and  $i+1$  is in state  $t$  at the time of sample  $i+1$  (Nichols et al. 1994, Lebreton et al. 2003). I define state  $s$  as breeding and state  $t$  as non-breeding. Breeding is an annually variable phenotypic trait. Therefore, females can change breeding states over time, analogous to moving between physically discrete areas. Whereas

standard encounter histories code presence or absence of individuals each breeding season, multi-strata encounter histories categorise animals further into different levels of breeding state, and in this way describe the pattern of breeding for each individual over time. Importantly, the model expresses the probability of encounters allowing for the uncertain state of animals during samples in which they were not re-sighted. In the base model, breeding probability followed a first-order Markov process i.e. the probability of breeding at time  $i+1$  depended only on earlier breeding efforts through the breeding state at time  $i$ . Therefore, reproductive rate was defined as the probability of being in breeding state at time  $i+1$ , conditional on surviving from time  $i$  to  $i+1$ .

### *Model structure*

Covariates were incorporated so that probabilities could be individual and time specific. With regard to re-sight rates, it was known *a priori* that re-sight rates ( $p$ ) varied over time and between Long Fjord and the Tryne area (Figure 5-1). Hence the re-sight model was stratified by time and area. A term for breeding state was used to test for different re-sight probabilities of females in different breeding state.

With regard to survival probability ( $\phi$ ), parameters for temporal variation were evaluated to test for inter-annual variation in the survival rates of adult females. A term for area was included to control for different degrees of fidelity to the study site (emigration). A term for breeding state was evaluated to test for survival costs of reproduction. Another term distinguished first and subsequent years that a seal was tagged and parous. Considering reproductive rate as a summary of the behaviour of site-faithful individuals, estimates should be independent of transient seals. All observations of marked, parous females were included in the dataset and the term for first and subsequent years tagged and parous was included to account for seals that failed to retain new tags or failed to establish in the study area.

Breeding probability ( $\psi$ ) was evaluated with regard to changes over time or by previous breeding state. We also assessed whether inter-annual variation in breeding probability was associated with two environmental parameters. The first of these was the Southern Oscillation Index (SOI), summarized as annual averages of monthly values from January to October. The SOI data were from the Australian Bureau of Meteorology and were the standardised anomaly of the mean sea level pressure difference between Tahiti and Darwin. The other environmental correlate was winter sea ice cover in Prydz Bay, expressed as the percentage cover of sea ice in July as estimated from SMMR-SSM/I data, and averaged over the Prydz Bay area (coast – 65°S, 60-90°E) (Comiso 2005).

### *Modeling procedures*

Multi-strata models often have multi-modal likelihood functions, so a simulated annealing algorithm incorporated in Program MARK ([www.cnr.colostate.edu/~gwhite/mark/mark.htm](http://www.cnr.colostate.edu/~gwhite/mark/mark.htm)) was used with different starting values to find the global maximum. Model selection procedures were based on Akaike's Information Criterion (AIC) (Burnham and Anderson 1992). Smaller AIC indicated better model fit. AIC differences greater than 2 indicated significant effects. Individual- and time-specific effects were expressed using a logit link function and linear models. Estimates were reported as  $\exp(\beta_2)$  i.e. the amount that the odds of survival are multiplied by for a one-unit change in the explanatory variable. An odds ratio of 1.0 was no effect. An odds ratio of 1.1 indicates that the odds increased by 10%. A large odds ratio indicated that probability associated with the numerator in the odds ratio tended to 1.0. In this way, the effect of each variable was described, independent of the level of other variables.

## RESULTS

### *The dataset*

In 1973 and 1974, 316 parous females were tagged (Table 5-1). Forty to sixty of those females were re-sighted per year over the next three years (1975-77), and marking methods were refined accordingly. More than 500 parous females were marked over the next five years (1978 to 1983) by which time the majority of the population had been tagged and less than 40 parous females required marking per year subsequently in the program. From 1980, females marked as pups began recruiting into the breeding population. In summary, the dataset consisted of 1,368 parous females, of which 1,138 were marked as adults (Table 5-1).

### *Evaluating models*

Combined, the best two models received 100% of the support (combined  $w_i = 1.000$ ) (Table 2). Both models had additive effects of first capture, time, area and state on survival probability, and re-sighting rates that varied in parallel between the two breeding states but that otherwise differed over time with the pattern of temporal variation in re-sight rates differing among areas. In the model receiving majority support ( $w_i = 0.624$ ) the transition probability between breeding states was just time dependent. In the second best model ( $w_i = 0.376$ ) the transition probability also depended on previous breeding state.

Table 5-1 Number of known-age (KA) and unknown age (UKA) females newly marked and parous each year in Long Fjord and the Tryne area, and the total number of parous females marked and re-sighted. Known-aged animals were marked at birth whereas unknown-age animals were marked usually as parous females. Parous is defined as sighted at least once in breeding state.

Year	Long Fjord		Tryne area		Total	Total
	KA	UKA	KA	UKA	Marked	Sighted
1973	0	123	0	11	134	134
1974	0	97	0	85	182	225
1975	0	1	0	0	1	62
1976	0	0	0	0	0	40
1977	0	1	0	0	1	57
1978	0	93	0	41	134	186
1979	0	52	0	66	118	233
1980	2	26	1	24	53	120
1981	2	31	0	34	67	164
1982	3	31	2	45	81	188
1983	5	24	1	50	80	261
1984	4	8	0	1	13	137
1985	3	6	0	14	23	137
1986	1	6	0	22	29	157
1987	14	9	1	7	31	179
1988	3	9	1	19	32	171
1989	9	4	7	15	35	184
1990	14	11	1	1	27	163
1991	4	3	5	3	15	154
1992	11	7	7	9	34	161
1993	13	8	0	5	26	142
1994	13	0	4	7	24	153
1995	14	4	0	10	28	140
1996	20	15	7	38	80	180
1997	0	0	0	0	0	0
1998	14	11	4	11	40	167
1999	16	2	8	11	37	173
2000	12	10	3	18	43	177
Total	178	591	52	547	1368	4326

Table 5-2 Model comparisons (a), where interaction effects (\*) and main effects (+) of various terms in the survival ( $\phi$ ), re-sight (p) and breeding probability ( $\psi$ ) models were quantified with regard to AICc, number of parameters (Npar) deviance and weight of support for the model ( $w_i$ ); Smaller AICc indicates the term improved model fit, and AICc<-2 or >+2 indicates significance.

a. Model comparisons	AICc	Npar	Deviance	$w_i$
$\phi$ (first+time+area+state) p(time*area+state) $\psi$ (time)	11859.79	107	6158.66	0.624
$\phi$ (first+time+area+state) p(time*area+state) $\psi$ (time+state)	11860.80	108	6157.57	0.376
$\phi$ (first+time+area) p(time*area+state) $\psi$ (time*state)	11877.14	131	6125.10	0.000
$\phi$ (first+time+area+state) p(time*area+state) $\psi$ (time*state)	11879.20	132	6125.03	0.000
$\phi$ (first+time+area+state) p(time*area) $\psi$ (time*state)	11884.15	131	6132.11	0
$\phi$ (time+area+state) p(time*area+state) $\psi$ (time*state)	11898.03	131	6145.99	0
$\phi$ (first+time+area+state) p(time*area*state) $\psi$ (time*state)	11898.80	184	6032.10	0
$\phi$ (first+time+area+state) p(time*area+state) $\psi$ (SOI+SIC)	11899.99	84	6247.10	0
$\phi$ (first+time+area+state) p(time*area+state) $\psi$ (SIC)	11907.64	83	6256.83	0
$\phi$ (first+time+state) p(time*area+state) $\psi$ (time*state)	11923.55	131	6171.51	0
$\phi$ (first+time+area+state) p(time*area+state) $\psi$ (state)	11932.98	83	6282.16	0
$\phi$ (first+time+area+state) p(time*area+state) $\psi$ (SOI)	11969.88	83	6319.07	0
$\phi$ (first+area+state) p(time*area+state) $\psi$ (time*state)	11980.46	108	6277.23	0
$\phi$ (first*time*area*state) p(time*area*state) $\psi$ (time*state)	12003.13	300	5874.39	0

Survival probability

The term distinguishing survival in first and subsequent years marked and parous ('First') decreased AICc by 18.83 (Table 5-2). This suggests different survival rates of 'new' compared to established breeders. The odds ratio with 95% confidence intervals (CI) of new breeders surviving was 0.55 (CI 0.43-0.70), which translated to an average 11.3% (constant on the logit scale) lower apparent survival in the first compared to subsequent years marked and parous. Different rates of apparent survival in new compared to established breeders could have been due to different rates of tag loss or emigration as well as real differences in rates of survival.

The term for area in the survival model decreased AICc by 44.3 units (Table 5-2). This suggests different rates of survival of females breeding in Long Fjord compared to the Tryne area. The odds of animals in the Tryne area surviving was 0.60 (CI 0.52-0.70) times that of animals in Long Fjord, which translated to an average 7% lower apparent survival in the Tryne area. Again, this could have been due to different rates of permanent emigration, as an alternative to real differences in survival.

The term for temporal variation ('time') in survival decreased AICc by 101.26 (Table 5-2), which indicates changes over time in apparent survival of parous females. The temporal trend was for



relatively low and variable survival in the first few years of the program, with higher, more constant survival rates post 1980-82 (Figure 5-2). Considering that pre-1980 many animals were newly tagged and various types of tags were being trialed, temporal variation in apparent survival could have been due to tag loss as opposed to evidence for a real shift in survival rates post 1980.

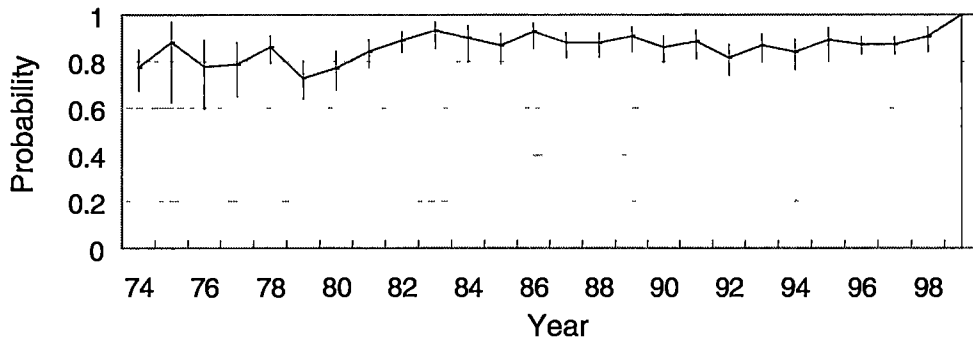


Figure 5-2 Survival probability of established, parous females in Long Fjord with upper and lower 95% confidence intervals as estimated by the most parsimonious model i.e.  $\phi$  (first + time + area + state)  $p$  (time \* area + state)  $\psi$  (time)

The term for breeding state ('state') in the survival model was equivocal ( $\Delta\text{AICc} = 2.06$ ) (Table 5-2). The fact that AICc provided no weight of evidence did not necessarily mean the effect size was zero. However, the odds ratio was close to one (1.04), with confidence intervals either side of parity (0.77-1.17), which showed more conclusively that breeding activity did not change the probability of survival. The term for breeding state was retained in the base model for a conservative set of model comparisons because the term had minimal effect on model fit ( $\Delta$  deviance = 0.072, Table 5-2).

#### *Re-sight probability*

To model re-sight rates, the interaction term for breeding state increased AICc by 19.59 units (Table 5-2) and thus was rejected. The main effect for breeding state decreased AICc by 4.95 units and thus was retained. This result indicates that re-sight rates differed for breeding and non-breeding state. The odds ratio of 3.12 (95% confidence intervals 1.38 – 7.60) indicates odds of re-sighting breeding animals were approximately three times higher than non-breeding animals, which translated to approximately 21.9% greater probability of re-sighting females when they were in breeding state.

It was known, *a priori*, that search effort varied over time and area. Thus these terms with interaction effects were included in the base structure of the re-sight model. Long Fjord females (in breeding state) had several years of re-sight rates less than 80%, and then high, relatively constant probability of

re-sight post 1986 for the rest of the study (Figure 5-3 top). In the Tryne area, re-sight rates were more variable - often less than 60% and exceeding 80% in only three years (Figure 5-3 bottom).

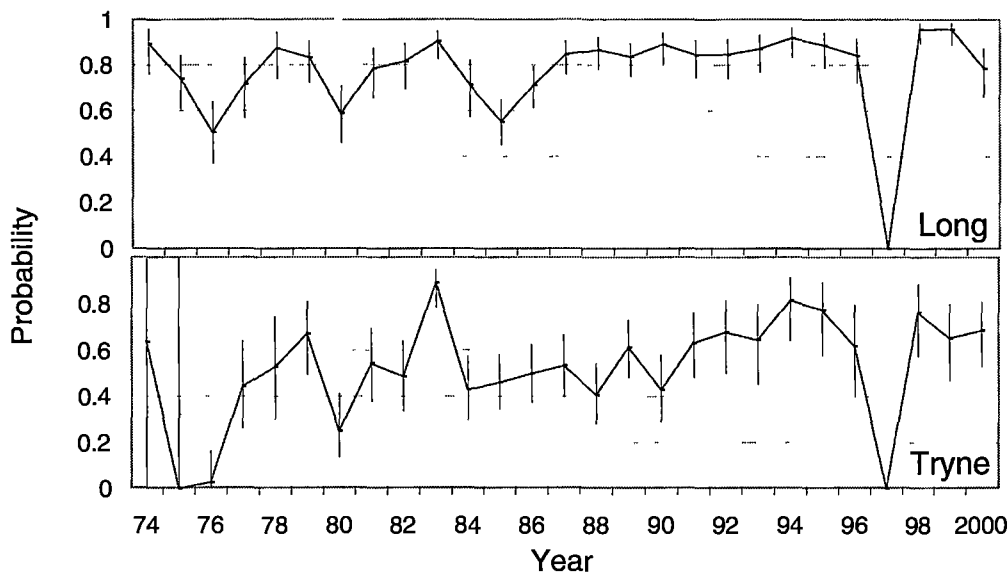


Figure 5-3 Re-sight probability of parous females in breeding state in Long Fjord (top) and the Tryne area (bottom) with upper and lower 95% confidence intervals as estimated by the most parsimonious model  $\phi$  (first + time + area + state)  $p$  (time \* area + state)  $\psi$  (time)

*Breeding probability*

In the model for breeding probability, the interaction term between breeding state and time was rejected ( $\Delta AICc = 18.41$ ) and the main effect for breeding state was equivocal ( $\Delta AICc = 2.06$ ) (Table 5-2). While the main effect for breeding state had an odds ratio of 0.88 (which translates to an effect size of more than 10%), the confidence intervals were either side of parity (0.70 and 1.11) indicating that there was no, clear evidence for fecundity costs of reproduction.

The term for temporal variation in breeding probability was highly significant, decreasing  $AICc$  by 72.2 points, and thus was retained in the model. The proportion of females in breeding state averaged 70%, and ranged from 53-88%. The temporal pattern was for high rates of reproduction in the 1970s, low rates in the early to mid 1980s high rates in the mid to late 1980s and then low rates of reproduction throughout the 1990s (Figure 5-4).

*Evaluating indices*

Compared with other methods of estimating reproduction (Figure 5-4), the temporal trend in the modeled time series was similar to simple ratio estimates of reproductive rate (Ratio 2), especially post 1980 when apparent survival was relatively stable. Model estimates were more similar to the ratio index when newly marked animals were excluded from the ratio (Ratio 1), since newly marked, parous females by definition had 100% probability of pupping, and the numbers of females newly marked varied from year to year according to the logistics of the program (Table 5-1). Temporal trend in pup counts showed little resemblance to other measures (Figure 5-4).

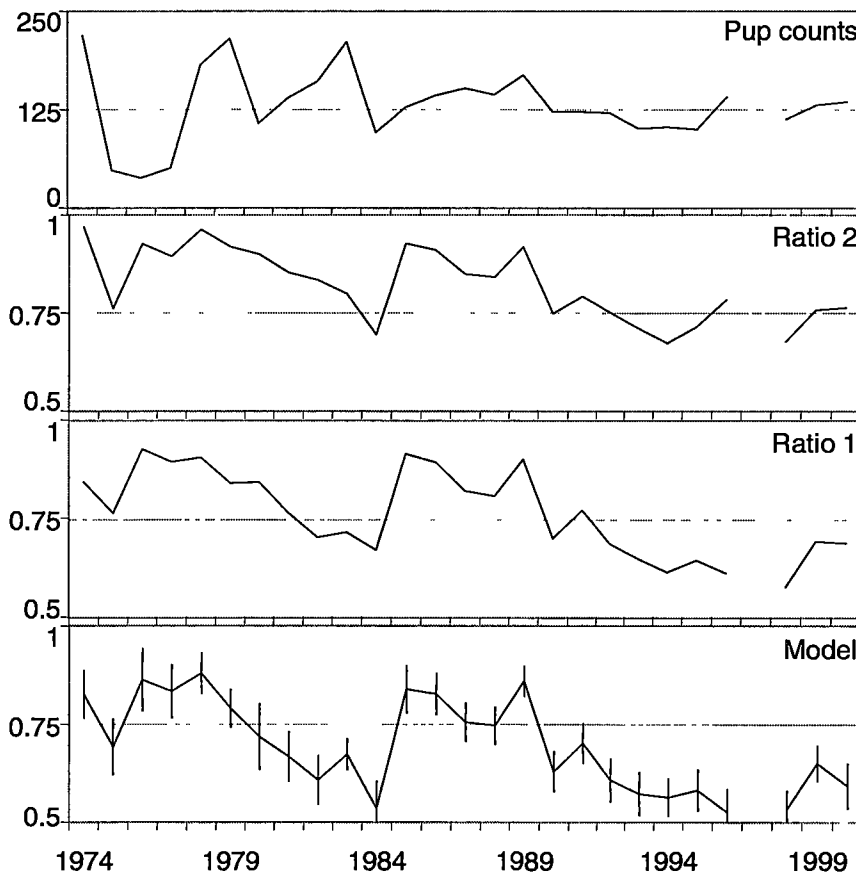


Figure 5-4 Probability of parous females being in breeding state (Model), estimated using the most parsimonious model and specifying upper and lower 95% confidence intervals, compared with estimates using the traditional estimates of reproduction including ratio of number of females sighted in breeding and non-breeding state (Ratio 2), ratio estimates excluding animals newly marked and parous (which had 100% probability of breeding by definition) (Ratio 1), and also number of pups that were tagged (Pup counts).

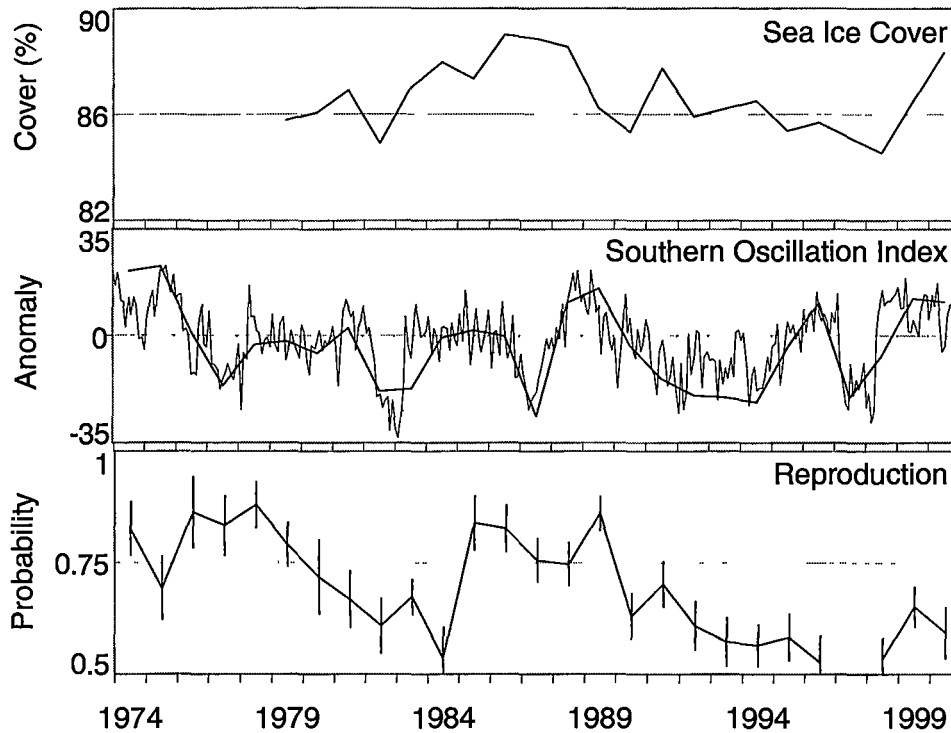


Figure 5-5 Probability of parous females being in breeding state (Reproduction) as estimated by the most parsimonious model (with upper and lower 95% confidence intervals) compared with monthly anomalies and annual average of monthly anomalies of the Southern Oscillation Index (SOI), and percentage sea ice cover (SIC) in July in Prydz Bay (coast - 65°S).

*Environmental correlates*

The models correlating environmental parameters with breeding probability yielded higher AICc's than models with individual parameters for each year of breeding, despite having fewer parameters (Table 5-2). This indicated that neither the Southern Oscillation Index nor sea ice cover accounted for a significant proportion of the variation in breeding probability. Examining the time-series (Figure 5-5), it is clear some features were synchronous but the synchronicity was not consistent. Low reproductive rate in 1982-1984 did coincide with the both El Niño and low sea ice cover in 1982. Similarly, low reproductive rates throughout the 1990's did coincide with the 1990-1995 and 1997-1998 El Niño conditions. Sea ice cover was also relatively sparse throughout this decade. On the other hand, the 1987 El Niño event was not associated with depressed breeding rates or a decrease in Prydz Bay sea ice cover (Figure 5-5).

## DISCUSSION

Multi-strata modeling showed, unequivocally, that the proportion of females in breeding state did vary over decadal time scales. The proportion of parous females in breeding state ranged from 0.53 to 0.88 per annum. This contrasts with the relatively high and stable rates of survival for adult females (Figure 5.2), and is similar to the magnitude of inter-annual variation in the proportion of pups surviving first year of life (Hastings et al. 1999, Cameron and Siniff 2004). The magnitude of inter-annual variation in both the proportion of females producing a pup, and the proportion of pups surviving their first year, reveals how tenuous each reproductive event is for Weddell seals. On the other hand, high and relatively stable survival rates result in long life span (approximately 30 years) (Bryden et al. 1984, Cameron and Siniff 2004). Average age of first reproduction is seven years (Hadley et al. 2006), and it is not unusual for relatively old animals to reproduce (S. Lake unpublished data). This leads to long reproductive tenure. Southern fulmars, Adelie penguins and Antarctic fur seals (*Arctocephalus gazella*) are also long lived with time-varying reproductive success (Whitehead et al. 1990, Lunn and Boyd 1993, Jenourvier et al. 2003, Forcada et al. 2005, Jenourvier et al. 2005). Commonly referred to as bet hedging (Stearns 1992), the life-history strategy corresponds with variable environments (Ferguson and Lariviere 2002). Indeed, physical conditions in the Southern Ocean are highly variable, and cyclic changes in sea-ice extent, sea-surface-temperature, and sea-surface pressure have been linked to ENSO and other principal modes of variability (Watkins and Simmonds 2000, Simmonds and King 2004, Turner 2004, Appendix 2).

### *The strategy of intermittent reproduction*

In naturally regulated populations, the physiological processes that regulate reproduction should be finely-tuned to maximize both number of viable offspring and the rate at which they reproduce since these behaviours, by definition, determine evolutionary fitness (Boyd 2000). Mammals, in general, are less likely to reproduce when nutritional stressed (Trites and Donnelly 2003). Feedback mechanisms include a complex web of hormones and other physiological systems. In humans, for example, nutritional stress results in cessation of ovulation. In pinnipeds, the crucial stage appears to be gestation via intra-uterine mortality. Several pinniped species have been shown to reproduce at rates less than 100% (Trites and Donnelly 2003). Examples in the phocid family include grey seals (*Halichoerus grypus*) which had low reproductive rate coinciding with low abundance of sandeels *Ammodytes dubius* (Pomeroy et al. 1999, Pomeroy and Duck 2000). Also ringed seal (*Phoca hispida*), whose average pregnancy rate was 55% over the period 1991-2000 which Stirling (2005) attributed to earlier break-up of sea ice in the Arctic. For Weddell seals specifically, terminal sampling at various stages of gestation has provided unequivocal evidence of intra-uterine mortality (Testa 1987).

The way in which intra-uterine mortality is employed differs between pinniped families and has consequences for costs of reproduction. Costs of reproduction are the energetic trade-off of weaning a viable pup, and include lower probability of surviving the year after reproduction and lower probability of reproducing the next breeding season (Stearns 1992). For both otarid and phocid families, viability of offspring is determined by the quantity of energy transferred from mother to pup (Baker and Fowler 1992, McConnell et al. 1992, McMahon et al. 2000, Crocker et al. 2001, Hall et al. 2001, Harding et al. 2005). Smaller pups at weaning have lower probability of surviving due to their limited capacity to dive (Burns et al. 1999, Hindell et al. 1999) and to thermoregulate (Harding et al. 2005). Seals in the otarid family differ from phocids in that they lactate over an extended period, and rely on energy gained during lactation to provision their young (Costa 1993). Thus, the condition of otarid seals during pregnancy is not an important determinant of the quantity of energy that will be available for lactation, and so viability of the fetus cannot be assessed during pregnancy. However, otarid seals do suckle the previous year's offspring whilst pregnant, and evidence suggests that, when foraging conditions are challenging, some otarid species terminate the fetus so as to wean the current pup at a viable mass (Boyd 2000, Trites and Donnelly 2003). The result is low probability of reproducing in consecutive years for some otarid species.

In contrast, phocid seals have short, intense lactation, and derive the majority of energy for lactation from maternal body stores (Wheatley et al. 2006). Successive reproductive attempts are temporally discrete. Thus the probability of weaning each fetus at viable mass can be assessed physiologically during pregnancy on the basis of maternal condition. Evidence suggests that when foraging conditions are challenging, some phocid species terminate pregnancy and thereby conserve energy, as opposed to proceeding with reproduction and depleting body stores when there is minimal chance of producing a viable pup (Boyd 2000). Even so, Siniff (1981) proposed that the energetic cost of lactation, whereby female Weddell seals lose up to 40% of body mass, could result in relatively low probability of breeding in consecutive years.

In this study, model comparisons neither confirmed nor refuted evidence for costs of reproduction, which was probably due to heterogeneity in individual quality (Clutton-Brock 1991, Pomeroy et al. 1999). If individuals with greater fitness are more likely to survive *and* to breed in consecutive years, then this can confound evidence for individuals not breeding in consecutive years, and not surviving when they breed. Individual variation in measures of fitness has been documented for Weddell seals (Hastings and Testa 1998, Hadley et al. 2006, Wheatley et al. 2006). An example from the Vestfold Hills' of exceptionally high measures of fitness is a female born in 1974 (the year after monitoring began). She had her first pup in 1980, did not pup the next year but did so every year after that, and was last re-sighted in the final year of field work still alive and pupping at age 26, having been parous

for 20 years and produced 19 pups: Exceptional considering that on average 70% of females reproduce per annum. I conclude that costs of reproduction for some individuals could have been counterbalanced by lack of costs for others.

This study did demonstrate an effect for lower apparent survival in the first year tagged and parous, suggesting survival costs of reproduction for primiparous females, consistent with Siniff's (1980) report of fecundity costs for primiparous Weddell seals. However, lower apparent survival in the first year parous could also have been due to higher rates of new tag loss (Testa and Rothery 1992), since many females were tagged when first sighted parous. Alternatively, newly parous females could have failed to establish as breeders in the study area. Conclusions are limited to stating that avoiding reproduction in consecutive years is not a dominant life-history strategy for Weddell seals, and that Weddell seal females have high rates of survival with no apparent survival costs for established breeders.

#### *Other measures of reproductive success*

Various performance indicators can be calculated using mark and re-sight data, and reproductive rate alone has been calculated several different ways (Siniff et al. 1977, Croxall and Hiby 1983, Testa and Siniff 1987, Testa et al. 1990, Testa et al. 1991, Hastings et al. 1999). In this study, the temporal trend in ratio of females sighted breeding and non-breeding did resemble model estimates, especially when the bias from newly marked parous females was removed. However, ratio methods overestimated the proportion of females in breeding state, and the temporal trend in pup counts showed little resemblance to other measures. We conclude that modeling is necessary to accurately estimate Weddell seal reproductive rate, at least at the Vestfold Hills.

In the past, when reproductive rate was difficult to quantify and not well understood (Testa et al. 1990), weaning mass and first year survival were monitored as indices of maternal condition (Hastings et al. 1999). However, accurately indexing maternal condition depends on eliminating other variables that change from year. This study showed that avoiding reproduction in consecutive years is not a dominant trait of Weddell seals. Thus we propose reproductive rate is the first variable implicated in the reproductive process. That does not make it the most important response, but results from this study indicate a large proportion of females do respond in this way. If a female sustains pregnancy, then maternal body condition will be evident in weaning mass (Wheatley et al. 2006), and weaning mass is related to probability of surviving the first year, as previously discussed. However, if most individuals reproduce in favourable years and only a sub-sample of females, biased toward high quality individuals, reproduce in poor years then there is inter-annual variation in the sample composition of

pups that are weaned and have a chance to survive their first year. Thus, it is not logical to monitor weaning mass or first year survival as an indicator of maternal body condition for species whose potential to reproduce is also influenced by maternal body condition.

### *Using reproductive rate as an index*

Interpreting reproductive rate with regard to the environment involves qualitative assessment of the temporal and spatial scales over which parous females derive nutrition. If a). reproductive attempts are temporally independent, and b). maternal body condition is the cue for terminating pregnancy, then the temporal window over which annual reproductive rate reflects foraging success is most likely during summer (Boyd 1991) but perhaps also during winter in the year reproduction is measured. Precise timing depends on the stage at which females terminate pregnancy. Bowen et al. (1981) suggested that female body condition is assessed continually through pregnancy. Boyd (1991) proposed that implantation, post mating and a 3 month diapause, is when environmental factors such as nutrition and climate exert their greatest influence on pregnancy. More research is necessary to define the timing.

Evidence compiled in this thesis support the premise that Weddell seals forage over relatively small spatial scales (10s or 100s of kilometers as compared to 1000s), specifically within Prydz Bay over the continental shelf (Green and Burton 1987, Chapters 2 - 4). Since Weddell seals forage over small spatial scales, different populations could simultaneously have different reproductive rates, depending on the small to medium scale environmental anomalies operating within each area (movement of upwelling zones for example). The reproductive time series of Weddell seals at the Vestfold Hills is probably indicative of foraging conditions within Prydz Bay.

### *Corresponding signals of flux*

In this study, a linear correlation with the Southern Oscillation index was not significant because periods of low reproduction endured for longer than El Niño events, possibly due to autocorrelation at lower trophic levels. Furthermore, El Niño events were not always associated with low reproductive rates, which could have been due to interaction effects between ENSO and other sources of variability in the Southern Ocean (Simmonds and King 2004). Better understanding of the teleconnections between ENSO and local physical and biological processes might elucidate the loose connections sometimes observed between ENSO and Weddell seal reproduction. In this study, winter sea ice cover was tested for correlation because it is an example of local phenomena that could



directly influence foraging behaviour. The resulting correlation was vague (Figure 5-5) but, once again, the sea-ice index was a composite measure over a long time and large area within which sea ice was heterogeneous. Weddell seals females may be affected by more specific aspects of sea-ice - the extent of coastal fast-ice during winter, for example: If seals use the fast ice as a safe base from which to forage, then changes in fast ice cover could determine traveling time between foraging and resting and ultimately the seals' energy balance and body condition (Chapters 3 & 4). Further studies of winter foraging behaviour will clarify the species' ecology.

Croxall et al. (2002) examined geographical inconsistencies in several Antarctic predator time-series to determine the geographical scale of forcing. Even though Weddell seal reproduction at McMurdo Sound has only been described using the ratio method (Testa 1987, Hastings et al. 1999), the published reports should be reasonably accurate since re-sight rates at McMurdo Sound have been much higher and less variable than at the Vestfold Hills (approaching 90% of adult females, Hastings et al. 1999, Cameron and Siniff 2004). Weddell seals at McMurdo Sound experienced low reproductive rates in 1977/78 and again in 1983/84 as did black-browed albatross, macaroni penguins and gentoo penguins at South Georgia (Croxall et al. 1988). The geographical breadth of that signal suggests the mechanism responsible for depression was similar in all cases, thereby implicating large-scale atmospheric or oceanic forcing. Indeed, the 1983/84 signal was also evident in the reproduction time-series from Weddell seals at the Vestfold Hills, and in Adelie penguin (*Pygoscelis adeliae*) reproductive parameters at the Vestfold Hills (Whitehead et al. 1990). The 1983/84 signal did coincide with a strong El Niño event in equatorial regions.

In contrast, low reproductive rates throughout the 1990s were experienced by Weddell seals at the Vestfold Hills but not at McMurdo Sound (Hastings et al. 1999), despite coinciding with more El Niño events. If the 1990's low in reproduction was in response to El Niño forcing, then the geographical scale of forcing was not to the extent of the Southern Ocean. There was perturbation in the 1990's in the vicinity of the Antarctic Peninsula that has been associated with krill cohort senescence and in turn sea ice conditions (Fraser and Hofmann 2003, Siegel 2005). That perturbation was not evident in time-series for Adelie penguins at McMurdo Sound, Mawson or Terre Adelie (Woehler et al. 2002, Jenourvier et al. 2005). Unfortunately, the monitoring program of Adelie penguins at the Vestfold Hills was terminated in 1989 (Woehler et al. 2002) and so an effect in the 1990s within the Prydz Bay region cannot be confirmed. This highlights the value of monitoring several species at various locations, and maintaining programs over time, for insightful interpretation of monitoring data. Irrespective of the cause, if nearly 50% of breeding females do not produce pups for a prolonged period of time, as observed for Weddell seals at the Vestfold Hills throughout the 1990's, then it does seem likely that population size will be affected.

### SUMMARY

Observations of seals and sea birds are valuable for environmental monitoring because they are among the few long time series that provide signals of variation in remote, marine environments. Mark and re-sight observations of Weddell seals (*Leptonychotes weddellii*) at the Vestfold Hills (68°S 78°E) form a considerable time series from Prydz Bay (1973-2000). The contribution of this particular project is in presenting a method by which quantitative evidence of reproduction and survival can be obtained from the mark and re-sight time-series, and also in presenting the time-series of reproductive rate for the Vestfold Hills population to date. The modeling method accounted for survival and re-sight rates when quantifying breeding probability. Model selection procedures indicate that annual reproductive rate of Weddell seals is a temporally precise index of foraging conditions, specific to the year of survey and, in this case, pertaining to the state of the environment in Prydz Bay. The resulting time-series showed that, throughout the 1990's, this population was relatively unproductive and this coincided with the longest El Niño event in the record of 113 years (1990-1995) closely followed by another very severe El Niño event (1997). Better understanding of the teleconnections between ENSO and more local physical and biological processes might elucidate the loose connections sometimes observed between ENSO and the reproduction of Weddell seals in the high Antarctic.

# Chapter 6

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## Synthesis and Conclusions

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A major concern in Antarctic ecosystems is global warming. In recent years, the El Niño -Southern Oscillation (ENSO) has shown increasing frequency and intensity of warm (El Niño) events (Trenberth and Hoar 1996, Watkins and Simmonds 2000), and the role of ENSO forcing in the Southern Ocean is now well documented for physical parameters (Kwok and Comiso 2002, Yuan 2004). Other large-scale physical phenomena operating in the Southern Ocean region seem to be changing in response to greenhouse gases and ozone depletion; the Southern Annular Mode for example (Watkins and Simmonds 2000, Liu et al. 2004, Marshall et al. 2004). Such changes in environment necessarily affect resident species. However, knowledge of each species' distribution and habitat is required to identify the causal links between population dynamics and the many possible proximate perturbations. Quantifying the dynamics of population processes presents various problems for long-lived animals, mainly with regard to observing sufficient cohorts to model the life-cycle. Weddell seals (*Leptonychotes weddellii*) at the Vestfold Hills have been marked and re-sighted for long enough to parameterize models that are both quantitative and demographically explicit. There should be few problems in the time-series, since a suitable marking method was established early on and the marked population has had minimal disturbance (Green et al. 1995). A similar program at McMurdo Sound has already established that Weddell seals have time-varying rates of reproduction and juvenile survival. In this thesis, annual rates of reproduction were quantified for the Vestfold Hills, and a new, more scientifically rigorous method of quantifying annual reproduction was described.

### *Diet composition*

A key finding from the diet study (Chapter 2) was that the prey types of Weddell seals are diverse. Variety in prey species demonstrates both flexibility in foraging behaviour and also the different types of marine fauna within this species' habitat. The study showed regional, seasonal and even fine-scale spatial variation in the diet. Fish species included the pelagic schooling notothenid, *Pleuragramma antarcticum*, as well as channichthyds and many species of benthic notothenid, all in the size range 9-21 cm standard length, which is typical of fish species over the Antarctic continental shelf (Williams and McEldowney 1990, Eastman 1993). There were also several invertebrate taxa, including decapod crustaceans (*Chorismus antarcticus* and *Notocrangon antarcticus*) that averaged 7 cm total length, squid (*Psychroteuthis glacialis*) that averaged 9 cm mantle length, octopus (*Paraleledone spp.*) that was small relative to squid, and mysids which occurred occasionally in large quantities, each one only 0.5 -1 cm total length. Whilst Weddell seals generally pursue and capture prey as individuals (Davis et al. 2003), in the case of mysids, seals must have captured several prey per mouthful. The large-bodied Antarctic cod (*Dissostichus mawsoni*), was not prevalent in this diet description, but Weddell seals at other

locations have been directly observed consuming Antarctic cod (e.g. Testa et al. 1985). When sampled on an ice-shelf nearby the continental slope, Weddell seals had consumed a suite of fish species from near the benthos over the continental slope (Plötz et al. 1991). When sampled in the subantarctic, they had consumed another suite of species typical of the sub-Antarctic (Casaux et al. 1997). In all but the most southerly area reported to date (McMurdo Sound), there have been several species dominant in the diet, which may minimize coupling between population dynamics and the abundance of any particular prey since the seals could compensate for declining abundance by switching to other prey types.

I assess the potential for Weddell seals to be part of the community of predators that forage on krill *Euphausia superba*, a keystone species in Antarctic ecosystems (Siegel 2005). Diet study showed that Weddell seals specialize on prey species from over the continental shelf, and this included benthic crustaceans at several locations. This demonstrates the potential for Weddell seals to consume krill in winter, when adult krill over-winter on the benthos of the continental shelf or on the under-side of sea ice (Siegel 2005). There was also evidence for bulk consumption of relatively small, pelagic prey types (juvenile notothenid fish c.a. 7 cm, and mysids c.a. 1 cm). This suggests that Weddell seals could consume krill when they swarm in upwelling regions over the continental slope or in the relatively warm, fresh water ellipse over the ocean surface in summer (Tynan 1999, Siegel 2005, Nicol 2006). The continental slope is only 80 km from the Vestfold Hills, less than 1 day's travel for a Weddell seal. There is no dynamic ice to partition the foraging of air-breathing predators at that time of year. I suggest it highly likely that Weddell seals consume krill if they are swarming within their foraging range. Yet this has never been reported. It could be that the distributions of krill and Weddell seals rarely overlap, but the lack of evidence for krill consumption is more likely due to research methods.

Feecal samples represent c.a. 1 day of feeding (Bowen 2000), and the samples collected in this and most other Weddell seal diet studies have been from coastal areas. At the Vestfold Hills, scats have been mainly from breeding areas where females with pups returned regularly for lactation, and females without pups may have been motivated to remain nearby for mating. Similarly in summer, samples have been from remnant fast ice where seals were hauled out to moult and rest. Despite an abundance of seals (Green et al. 1995), tagged females of reproductive age are rarely sighted in summer on areas of remnant fast-ice at the Vestfold Hills (S. Lake, unpublished data): Presumably those seals are foraging in the open ocean further offshore. If breeding females do not haul out on coastal fast ice in summer then faecal sampling is not going to be an effective method of determining their diet. Other methods of diet analysis should be utilised (e.g. Burns et al. 1998).

### *Distribution and movement of Weddell seals in winter*

The southern region of the Vestfold Hills is adjacent to the Sorsdal Glacier (Figure 3-1). Deep water seaward of that glacier is associated with a lead of open water that forms immediately adjacent to fast ice. That lead penetrates northwest, from the glacier and along the edge of the broadening strip of land-fast ice, into Prydz Bay (Worby et al. 1998, Micheal and Hill 2002). Hypothetically, seals use that lead to commute offshore, since haul-out sites in the vicinity of the glacier were actually at the fast ice edge. Haul-out sites further north, in the central and northern regions, were within the tract of ice at cracks and icebergs. Since individual variation in foraging range has been documented (Testa 1994), it is plausible to suggest that seals were foraging both beneath both fast ice and further offshore in dynamic ice, perhaps remaining in dynamic ice so long that they were rarely encountered at the Vestfold Hills. Consistent with this hypothesis, there was an influx of animals in September that were encountered at the ice edge in the southern Vestfold Hills (S. Lake, unpublished data). Presumably those seals came from offshore and were waiting to move into breeding colonies.

Both tracking and distribution studies demonstrate that Weddell seals are able to find winter retreat in land-fast ice as an alternative to migrating north for winter. Familiar fast ice may be relatively safe habitat for Weddell seals in winter because it is more constant than dynamic ice, thus enabling them to reliably locate tunnels through the ice (c.a. 2 m thick) (Kooyman 1975). Cooperative use of breathing holes could aid navigation (Wartzok et al 1992) and minimize the tooth wear incurred by rasping ice to maintain open water (Stirling 1969). The hypothesis that Weddell seals prefer to rest on fast ice is supported by relatively few sightings from ship surveys.

If Weddell seals forage in dynamic ice whilst returning to fast ice to rest then I propose that fast ice extent could be an important determinant of inter-annual variation in nutritional state, hypothetically indexed by reproductive rate. North of the Vestfold Hills, to the Davis Ice Shelf, the coast is fringed by fast ice in some years but has only patches of fast ice in others (Micheal and Hill 2002). If seals use that fast ice as a base from which to forage then changes in fast ice cover could determine traveling time between foraging and resting areas and perhaps ultimately, due energy balance or even safety considerations, the extent of fast-ice platforms could determine winter foraging range.

### *The mark and re-sight data*

The multi-strata model of Weddell seal reproductive rate showed, unequivocally, that the proportion of females in breeding state varied over time. The proportion ranged from 52.4 to 85.9%; which contrasts with the relatively high and stable rates of annual survival. If the viability of Weddell seal reproduction is assessed on the basis of maternal condition at some stage during parturition, then

reproductive rate can be perceived as an index of net foraging success, prior to the breeding season and post weaning the previous pup, thus specific to each year of survey. With regard to spatial considerations, the evidence for a limited foraging range (Chapters 2-4) suggests that this time-series is indicative of environmental conditions within Prydz Bay. Foraging range largely determines the extent to which small to medium scale environmental anomalies (movement of upwelling zones for example) affect the condition of a population.

Croxall et al. (2002) examined geographical inconsistencies in Antarctic predator time-series to determine the geographical scale of forcing. Similarly, Weddell seal datasets from opposite sides of Antarctica are directly comparable. To date, the reproduction time series from McMurdo Sound has only been described using the ratio method (Testa 1987, Hastings et al. 1999) but this should be reasonably accurate since re-sight rates at McMurdo Sound approach 90% of adult females (Hastings et al. 1999, Cameron and Siniff 2004). Weddell seals at McMurdo Sound experienced low reproductive rates in 1977/78 and again in 1983/84 as did black-browed albatross, macaroni penguins and gentoo penguins at South Georgia (Croxall et al. 1988). The geographical extent of reduced productivity suggests that the mechanism responsible for the depression must have been similar in all cases, implicating large-scale atmospheric or oceanic forcing. Indeed, the 1983/84 signal was also evident in the reproduction time-series from Weddell seals at the Vestfold Hills (Chapter 6), and in Adelie penguin (*Pygoscelis adeliae*) reproductive parameters at the Vestfold Hills (Whitehead et al. 1990). These population perturbations did coincide with a strong El Niño event in equatorial regions.

In contrast, the low reproductive rates experienced by Weddell seals at the Vestfold Hills throughout the 1990s were not evident for Weddell seals at McMurdo Sound (Hastings et al. 1999), despite coinciding with more El Niño events. If the 1990's low in reproduction was in response to El Niño forcing, then the geographical scale of forcing was not to the extent of the Southern Ocean. There was perturbation in the 1990's in the vicinity of the Antarctic Peninsula that has been associated with krill cohort senescence and in turn diminishing sea-ice extent in the peninsula region (Fraser and Hofmann 2003, Siegel 2005). That perturbation was not evident in time-series for Adelie penguins at McMurdo Sound, Mawson or Terre Adelie (Woehler et al. 2002, Jenouvrier et al. 2005).

Unfortunately, the monitoring program of Adelie penguins at the Vestfold Hills was terminated in 1989 (Woehler et al. 2002) and so an effect in the 1990s in the Prydz Bay region cannot be confirmed. This highlights the value of monitoring several species at various locations, and maintaining programs over time.

In this study, a linear correlation with the Southern Oscillation Index was not significant because periods of low reproduction endured for longer than El Niño events, and not every El Niño event was associated with low reproductive rates. More years of monitoring Weddell seals and other higher-

trophic level predators, simultaneous with remote sensing and insitu measurements of environmental parameters, might elucidate the loose connections sometimes observed between ENSO and Weddell seal reproduction. At this stage, it is simply noted that the longest El Niño event in the record of 113 years (1990-1995) (Trenberth and Hoar 1996), closely followed by another very severe El Niño event (1997), coincided with relatively poor productivity levels for this Weddell seal population throughout the last decade of monitoring. This could be just one example of how increasing frequency and duration of El Niño (warm events) has already affected Antarctic marine ecosystems. For population viability analysis specific to Weddell seals, more work is needed to associate the probability of reproduction with aspects of the environment because, in periodic environments, population projections require both a model describing temporal variation in vital rates and a function that associates sets of vital rates with each state of the environment (Caswell 2001).

### *Conclusions*

Mark and re-sight observation are one of the best sources of data for population models, especially for species such as Weddell seals that are readily approachable and identifiable as individuals, and especially in areas such as Long Fjord that are equivalent to an island population. In the past, strategic decisions have been made by CCAMLR (Convention on the Conservation of Antarctic Marine Living Resources) with regard to the CCAMLR Ecosystem Monitoring Program (CEMP). Weddell seals weren't given priority for monitoring because it was presumed they did not eat krill, which was the species being harvested at the time. Now, there are other, well recognized anthropogenic influences in the Antarctic. Global warming, specifically the increase in frequency and intensity of El Niño events, was the anthropogenic change discussed in this thesis. Reproductive rate is proposed as an index to capture and condense the effect of such phenomenon on the state of the environment as perceived by this predator species. This index can be measured on regular basis and interpretation with regard to the environment will improve as tracking and foraging data accumulate.

In this thesis, it has been my objective to make thorough and quantitative analyses of the Vestfold Hills data, and interpret these with regard to the species' ecology, to enable relevant scientific committees to decide whether or not Weddell seal monitoring should continue. The worth of long-time series data increases exponentially with time and it is imperative that the worth of all existing programs be properly assessed if we are to comprehend the ecosystem consequences of climate change. Already, as a consequence of Chapter 5, the Weddell seal mark and re-sight program at the Vestfold Hills has resumed after a break of six years in field work. The missing years of observation can be incorporated in models of reproduction. Cohorts that have not been marked are only relevant



to estimating juvenile survival. What's required for estimating reproductive rate is maintaining the marking status of breeding females, and also re-sighting individual females in consecutive breeding season and recording their breeding state.

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# Appendix

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# Antarctic sea-ice velocity as derived from SSM/I imagery

P. HEIL,<sup>1,2</sup> C.W. FOWLER,<sup>3</sup> S.E. LAKE<sup>4</sup>

<sup>1</sup>*Australian Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia*

<sup>2</sup>*Antarctic Climate and Ecosystems CRC, University of Tasmania, Private Bag 80, Hobart, Tasmania 7001, Australia*  
E-mail: [petra.heil@utas.edu.au](mailto:petra.heil@utas.edu.au)

<sup>3</sup>*Colorado Center for Astroynamics Research, Aerospace Engineering Sciences Department, University of Colorado, Boulder, CO 80309-0431, USA*

<sup>4</sup>*Institute for Antarctic Southern Ocean Studies, University of Tasmania, Private Bag 77, Hobart, Tasmania 7001, Australia*

**ABSTRACT.** Sea-ice velocities derived from remotely sensed microwave imagery of the Special Sensor Microwave/Imager (SSM/I) have been analyzed for changes over time in Antarctic sea-ice velocity, for the period 1988–2004. Year-to-year variability in mean Antarctic annual SSM/I-derived ice speed is small (17 year standard deviation (SD) =  $0.008 \text{ m s}^{-1}$ ), with greater interannual variability in the zonal (eastward positive) velocity components (17 year SD =  $0.016 \text{ m s}^{-1}$ ). Seasonally, minimum ice speed is encountered during summer, when nearly all Antarctic sea ice is within the marginal ice zone. Ice motion peaks during winter and spring, due to high velocities encountered in the outer pack of the seasonal sea-ice zone. The correlation ( $R^2 = 0.47$ ) between winter Southern Annular Mode (SAM) and mean winter ice speed highlights the importance of atmospheric forcing on sea-ice dynamics. The spatial pattern of the correlation of the standardized SAM index with the June–November ice speed exhibits a wave-3 pattern, which matches the sea-level pressure distribution. Sea-ice speed in the upstream regions of quasi-stationary centres of low sea-level pressure is likely to increase (decrease) during high (low) SAM years, and the opposite for sea-ice speed in the downstream regions of the centres.

## INTRODUCTION

Climate research, including that of polar regions, rapidly produces new hypotheses and provides interpretations of observational and modelled data. Interannual to decadal atmospheric variability in the southern polar region may be quantified by the Southern Annular Mode (SAM) index (Thompson and Wallace, 2000) or the Antarctic Oscillation (AAO; Gong and Wang, 1999). Gong and Wang (1999) interpreted this phenomenon as the exchange of mass between the mid- and higher latitudes due to the air-pressure gradient between  $40^\circ \text{S}$  and  $65^\circ \text{S}$ .

In the Southern Ocean, changes in SAM index can be thought to cause significant sea-ice and ocean circulation anomalies by way of stronger westerly winds, and thus increased Ekman transport of sea ice northwards and also eastwards, with strongest signals in the Pacific sector (Hall and Visbeck, 2002). The index was low during the 1960s and into the 1970s, but from the early to mid-1970s it increased (Hurrell and Van Loon, 1994; Meehl and others, 1998; Gong and Wang 1999). Thompson and Solomon (2002) interpreted large-scale atmospheric changes south of  $20^\circ \text{S}$  as a consequence of changing strength of the polar vortex. They suggest that the change in sign of the SAM is in response to ozone depletion. This is in agreement with Marshall and others (2004), who suggest that increases in greenhouse gases also are a contributing factor.

Consequent to these findings, we need to explore if there are any traceable changes in the state of the Antarctic sea ice. Sea ice is an integral part of the polar climate system, that interacts with ocean and atmosphere on various timescales. The evolution of sea ice is determined by environmental factors, chiefly by atmospheric temperature, winds and incoming solar radiation near the surface, oceanic currents including tidal and inertial forcing, and the heat content within the upper ocean (e.g. Hibler, 1979).

While, on seasonal scales, sea-ice concentration and extent are largely driven by the thermal budget at the ocean–atmosphere interface, interannual changes are generally due to dynamic variability within the patterns of atmospheric and oceanic circulation. Sea-ice motion depends largely on the integrated effect of oceanic and atmospheric momentum transfer but is also influenced by internal ice properties, which in turn are affected by thermodynamic processes. Sea-ice dynamics is important, as it redistributes the pack, hence influences ice extent, concentration and thickness distribution. Via these processes, sea ice interacts with other components of the climate system, such as surface albedo, or heat and moisture exchange at the ocean–atmosphere interface, and also the Southern Ocean biota. To fully assess the state of the sea ice, information on sea-ice velocity is required covering those temporal and spatial scales relevant to climate processes.

Few data are available on the past state of sea ice. Remote-sensing instruments such as the Scanning Multi-channel Microwave Radiometer (SMMR; 1979–87) and the Special Sensor Microwave/Imager (SSM/I; 1987–present) provide bidaily and daily, respectively, composites of sea-ice concentration. Using data from 1979 to 1998, Zwally and others (2002) determined that the total Antarctic sea-ice extent (for concentrations above 15%) has increased by  $(0.98 \pm 0.37)\% \text{ decade}^{-1}$ , and that the total sea-ice area has increased by  $(1.26 \pm 0.43)\% \text{ decade}^{-1}$ . Regional differences are apparent: ice extent has increased in the Weddell Sea, the Pacific Ocean sector and the Ross Sea, while a slight decrease in the Indian Ocean sector and a stronger decrease in the Bellingshausen and Amundsen Seas sector have been recorded. See Liu and others (2004) or Parkinson (2004) for details.

Emery and others (1997) have previously presented mean sea-ice motion derived from SSM/I data for 1988–94. They reported strong, coherent patterns of ice motion consistent



with wind directions. Their study did not assess the inter-annual variability in sea-ice motion. Liu and others (2004) analyzed changes in the state of Antarctic sea ice (including ice velocity) using SMMR and SSM/I data and related those to changes in atmospheric forcing.

In this study, we extend the SSM/I-derived ice-motion time series to cover the interval 1988–2004 but exclude SMMR-derived ice motion, as our analysis showed that the time series are not compatible. Reprocessing and validation of the SMMR-derived motion data is currently underway. We examine the SSM/I-derived data for temporal changes in ice motion as well as the regional nature of change; the modes of variability in the motion data and the potential for these modes to be related to atmospheric phenomena; and interpret the findings with regard to temporal changes in sea-ice extent and concentration.

### SEA-ICE MOTION FROM PASSIVE MICROWAVE IMAGERY

The broad-scale features of sea-ice drift can be derived effectively using consecutive satellite imagery together with the maximum cross-correlation method (e.g. Fowler, 1995; Emery and others, 1997). This yields a composite product of sea-ice motion on an Eulerian grid with global coverage where passive microwave data are available. Prior to satellite techniques, sea-ice motion was measured by Lagrangian methods (e.g. with ice-moored vessels or drifting buoys). Spatial accuracy and temporal resolution of in situ measurements (e.g. drifting buoys) are superior to measurements derived from passive microwave imagery, but the latter is extremely valuable as it covers most of both polar sea-ice zones and is available daily.

The gridded horizontal resolution of the SSM/I 85.5 GHz (37 GHz) data is 12.5 km by 12.5 km (25.0 km by 25.0 km). The maximum cross-correlation method (e.g. Emery and Thompson, 1998) was applied to derive sea-ice velocity as a temporal function of the spatial translation of features within the imagery. A search window of 125 km by 125 km was selected with a search range of 90 km. The derived velocity product using combined data from the 85.5 and 37 GHz channels has a resolution of 25 km by 25 km. Using the daily SSM/I time series, a continuous range from  $-1.04$  to  $1.04 \text{ m s}^{-1}$  may be detected in both horizontal ice-motion components. This range envelopes all ice motion within the physically plausible range of sea-ice velocities.

In a previous study, daily buoy-derived sea-ice motion was compared with daily composites of SMMR- and SSM/I-derived ice motion off East Antarctica (Heil and others, 2001). Large-scale patterns in sea-ice drift compared well, while the comparison along the buoy trajectory showed that satellite-derived ice motion is up to 40% less than that derived from buoy data. Thus, in this study, the satellite-derived data have been calculated using a larger search area (see previous paragraph), as suggested by Heil and others (2001), to allow the detection of high ice speeds in this dataset.

We assess the revised satellite-derived ice-velocity data by comparison with direct observations of sea-ice motion. In situ ice-motion data have been obtained from the International Programme on Antarctic Buoys (IPAB) for the years 1995–2000. Buoy data, available for most regions around the Antarctic and covering all seasons, have been used here. The drift trajectories of daily buoy motion have been traced

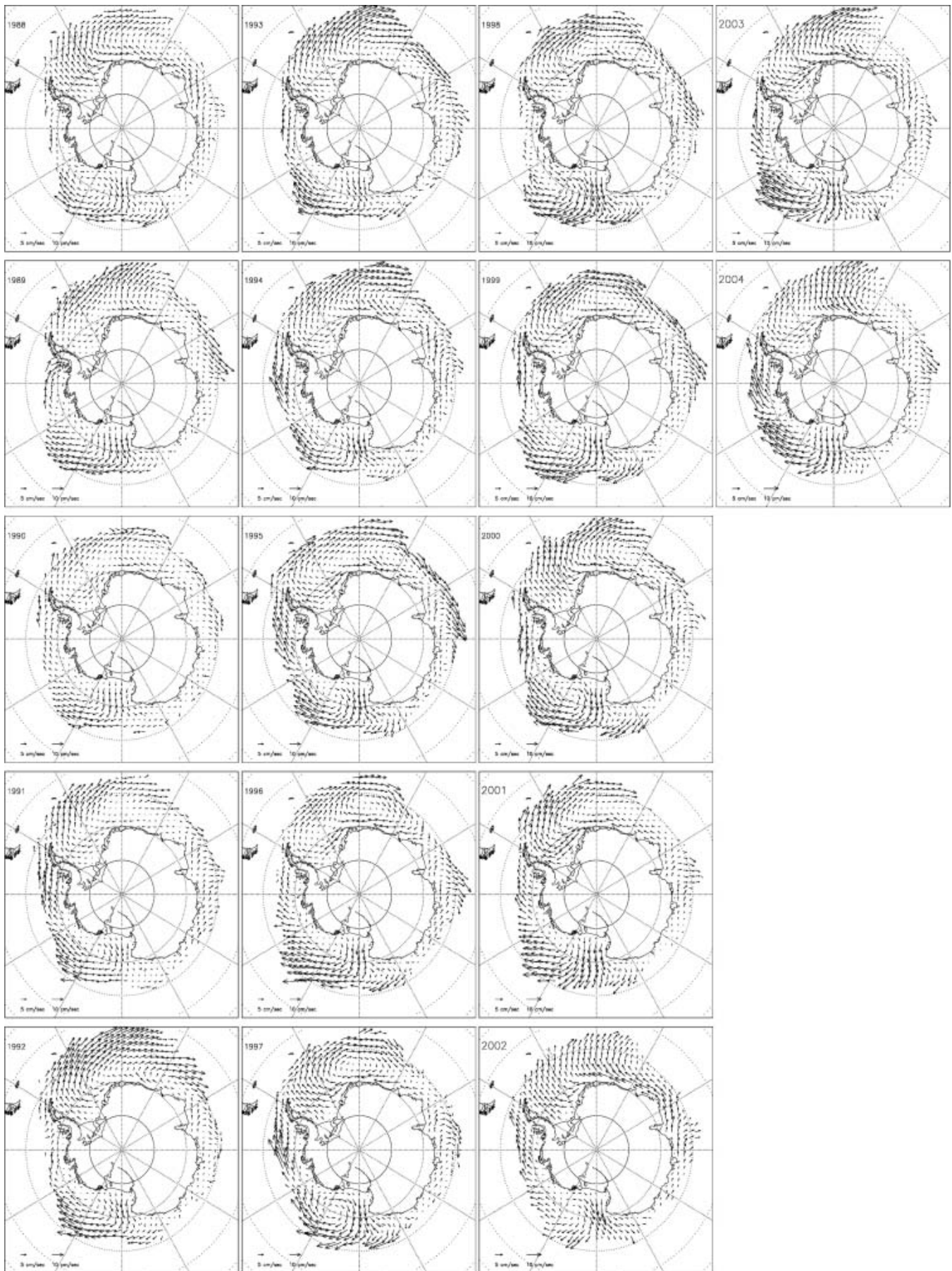
in the daily composites derived from the passive microwave imagery. For the circum-Antarctic average, the IPAB ice-drift speeds exceed those derived from SSM/I passive microwave imagery by about 30%. The root-mean-square error of daily SSM/I composites compared to buoys is about  $0.096 \text{ m s}^{-1}$ , with the bias below  $0.025 \text{ m s}^{-1}$ . This discrepancy might be due to non-coincident observations, as the SSM/I data have been taken over a 24 hour interval centred at the buoy's 00:00 UT observation, or due to the difference in spatial footprint of the velocity data: buoy observations are effectively point data, while SSM/I velocities are given on a 25 km by 25 km grid. For further comparison of sea-ice velocities, see Heil and others (2001).

### THE SPATIAL PATTERN OF ANTARCTIC ICE MOTION

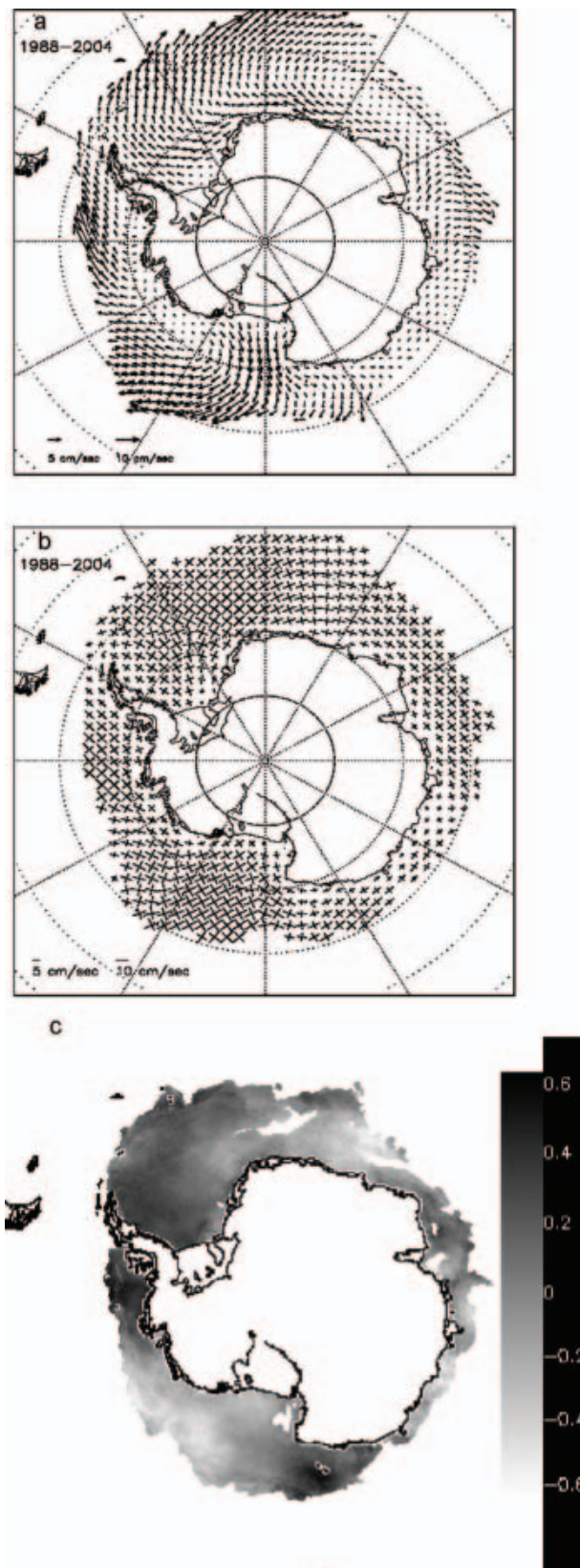
As with the ice extent and ice concentration, there are regional differences in the sea-ice velocity. The sea ice responds to atmospheric and oceanic forcing, which vary both spatially and temporally. We present the spatial pattern of mean June–November ice velocity for each year (Fig. 1). June–November mean data have been chosen to cover the time when the Antarctic sea ice is at or near its maximum equatorward extent. It is worth noting that during June–November the effect of atmospheric moisture on the 85.5 GHz SSM/I channel is considerably less than during summer (Gloersen and Cavalieri, 1986), hence avoiding significant loss in accuracy of the combined 85.5 and 37 GHz ice-velocity product.

While the general pattern of sea-ice velocities around the Antarctic repeats from year to year, Figure 1 indicates that June–November ice velocities for 1990, 2003 and 2004 are lower than those in other years. During those years, ice velocities are low in the East Antarctic and to a certain degree also in the large Antarctic gyres. Those years coincide with low circum-Antarctic ice extent (e.g. Parkinson, 2004). This implies that there is less sea ice along the outer pack, where one generally encounters high ice velocities, this being the reason for overall slower ice speed. During most other years, higher ice speeds were identified in individual regions, often near the outer ice edge in the eastward limb of the Weddell, Ross or Amundsen Sea, and occasionally also near the outer edge of sea ice north of Prydz Bay and in the northward limb of the Ross Sea Gyre.

The mean June–November sea-ice velocity for 1988–2004 is shown in Figure 2a to explore the pattern of Antarctic ice velocity over that interval. The net eastward motion in the outer pack dominates the zonal component. There is a near-continuous band of eastward ice motion, which is only disrupted in the region 115–145° E. The latter region is identified as an area of minimum thickness in the circumpolar band of Antarctic sea ice. The northward ice extent in this region is generally around 450 km or less, considerably less than the average northward ice extent of about 620 km around Antarctica. The eastward flow of sea ice is strongest from 180° E to 290° E north of the Ross and Bellinghausen and Amundsen Seas. The Ross Sea region also has the fastest northward movement of Antarctic sea ice. Net movement north and east of sea ice in this sector may pertain to the decrease in ice extent (Zwally and others, 2002) and also in annual duration of sea-ice cover (Parkinson, 2004) observed in the Bellinghausen and Amundsen Seas region.



**Fig. 1.** Mean June–November sea-ice drift derived from SSM/I imagery for 1988–2004. For clarity, only every eighth vector is shown.



**Fig. 2.** (a, b) Mean sea-ice speed derived from SSM/I imagery for June–November 1988–2004 (a) (for clarity, only every sixth vector is shown) and its standard deviations (b) (both in  $\text{m s}^{-1}$ ). (c) Correlation coefficient of mean sea-ice speed with SAM index for June–November 1988–2004. A minimum of 20 independent pairs of passive microwave imagery are required for any gridcell to be included in this representation.

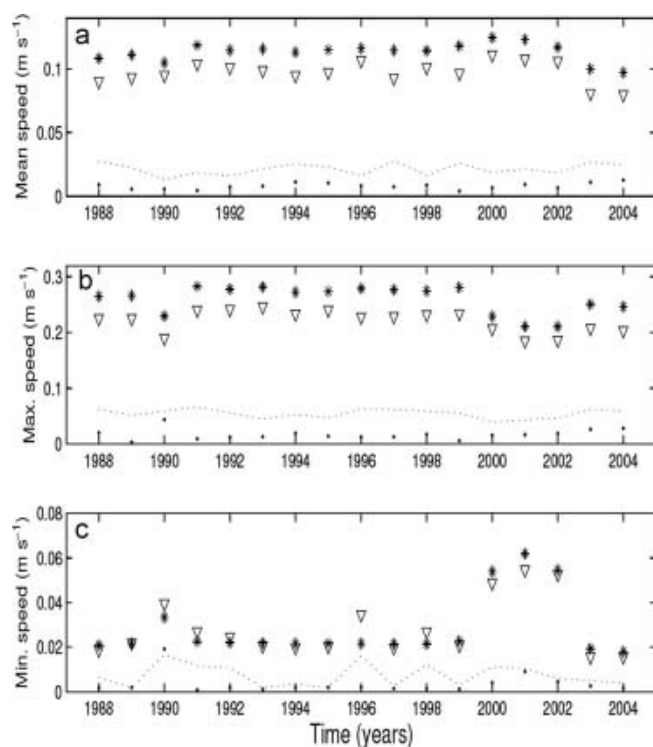
There is also strong northward movement in the outer Weddell Sea, but in this region the north- and eastward motion of ice seems to be balanced by the westward drift of sea ice into the Weddell Sea Gyre from the East Antarctic coast. Westward ice motion peaks in the region from  $15^\circ \text{W}$  to  $45^\circ \text{E}$ , where the coastal current is steered to the south by bathymetric features, such as the Riiser-Larsen Ridge. We should note here that due to masking effects the passive-microwave-derived ice velocity data do not extend all the way to land but stop about 75 km short of the coast.

Figure 2b depicts the interannual variability in sea-ice motion for the axes, along which the largest change occurred. The variability in ice motion is largest in the eastern Ross Sea and northern Weddell Sea. There the variability for both velocity components is of similar magnitude. Off East Antarctica, interannual variability in the zonal velocity component exceeds that of the meridional component, and the opposite in the Bellingshausen Sea. The magnitude in the standard deviation is controlled dynamically.

The correlation between the standardized (to 1 SD) SAM index and the mean June–November ice speed (Fig. 2c) exhibits a wave-3 pattern. For 1988–2004, sea-ice speed and standardized SAM index exhibit negative correlation in the eastern Ross Sea and Amundsen Sea, along  $10^\circ \text{W}$  to  $45^\circ \text{E}$ , along  $100^\circ\text{--}140^\circ \text{E}$  and also in the eastern limb of the Prydz Bay Gyre. Positive correlations are found in large parts of the Weddell Sea and to a lesser degree in the Bellingshausen Sea, along  $45^\circ\text{--}70^\circ \text{E}$  and  $145^\circ\text{--}165^\circ \text{E}$ . This wave-3 pattern projects onto the surface-pressure distribution (e.g. Hurrell and Van Loon, 1994) as well as the density distribution of Antarctic cyclone centres (e.g. Simmonds and Keay, 2000): centres of low surface pressure and also peaks in winter cyclone activity are found over the southern Ross Sea, southeastern Weddell Sea and southern Prydz Bay. Our analysis consistently reveals positive correlations between ice speed and standardized SAM index in each of the upstream regions of the low-pressure centres, and negative correlations in the downstream regions of the low-pressure centres. This indicates that changes in the atmospheric pressure field modify the Antarctic sea-ice speed bifold: in regions upstream of low-pressure centres ice speed increases with increasing SAM index, but in downstream regions the ice speed decreases with increasing SAM index. This dichotomy is likely to be associated with the strengthened clockwise rotation of low-pressure centres during high SAM, which induces northward (southward) deflection in the upstream (downstream) pack, and hence a translation of the pack into regions of higher (lower) ice speed.

### ANTARCTIC SEA-ICE MOTION, 1988–2004

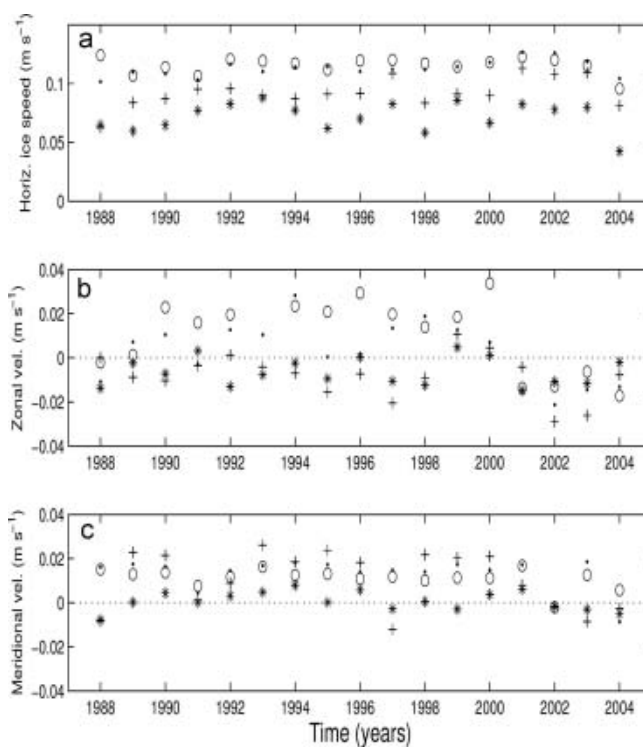
The long-term average Antarctic SSM/I-derived ice speed is about  $0.095 \text{ m s}^{-1}$ . During 1988–2004, interannual variability in circum-Antarctic mean annual ice speed is as large as 28% of its overall magnitude. There was a slight net rise of  $0.001 \text{ m s}^{-1} \text{ a}^{-1}$  (significant at the 90% confidence interval; Kreyszig, 1988) in the mean annual ice speed from 1988 to 2000 (Fig. 3a). In 2003 and 2004, ice speed dropped back to its lowest values for the 1988–2004 record (Fig. 3, triangles). The analysis of circumpolar net ice speed derives that the trend of the 1988–2004 annual mean is not significant at the 90% confidence interval.



**Fig. 3.** Annual (triangles) and mean June–November (stars) mean (a), maximum (b) and minimum (c) ice speed for all of the Antarctic sea-ice zone. Standard deviations are shown as dotted line (annual) and dot points (mean June–November).

The mean June–November ice speed for 1988–2004 is  $0.113 \text{ m s}^{-1}$ , with an interannual pattern of change similar to the mean annual pattern. For all years, the mean and maximum June–November ice speed (Fig. 3, stars) exceeds the annual mean and maximum, respectively. Due to the extreme northern position of Antarctic ice extent during winter and spring, at these times ice drift is affected by the oceanic and atmospheric regimes in the heart of the Southern Ocean, including the strong eastward flow of the surface ocean along the southern edge of the Antarctic Circumpolar Current.

The analysis of seasonal ice velocities (Fig. 4a) confirms that circum-Antarctic mean ice velocity is lowest during summer (December–February), and that ice speed increases in autumn (March–May) and reaches maximum speed during winter (June–August) and spring (September–November). Mean horizontal velocities during winter and spring are generally of similar magnitude for each year. The magnitude of the interseasonal changes (summer to winter) is more than twice that of the interannual variability within each seasonal component. Zonal (Fig. 4b) and meridional (Fig. 4c) velocities exhibit significant interannual variability within each season. This year-to-year variability of the seasonal velocity components includes reversal of the flow direction, especially for the zonal velocity: Summer and autumn zonal ice motion is mostly net westward from 1988 to 2004. Winter and spring zonal ice motion is net eastward from 1989 to 2000 and net westward before and after those years. The net westward ice motion during summer and autumn agrees with observations of the sea-ice distribution, with most of the sea-ice-covered area to the south of the Antarctic Divergence, where the flow is westward with the Antarctic coastal current (e.g. Orsi and others, 1995). Net southward ice



**Fig. 4.** Seasonal mean horizontal ice speed (a), zonal (b) and meridional velocity (c) for December–February (stars), March–May (crosses), June–August (dots) and September–November (circles).

motion (Fig. 4c) is rarely observed for any season. For the few summer and autumn seasons to exhibit net southward ice motion, comparison with spatial distributions of sea-ice concentration (courtesy US National Snow and Ice Data Center (NSIDC)) shows that during these seasons the pack ice was largely limited to the large cyclonic embayments.

Further analysis of the 17 years of circum-Antarctic SSM/I ice-velocity data reveals that major changes in the horizontal ice speed and the zonal and meridional ice velocities take place at annual and semiannual periods. The Fourier analysis also indicates an 8.2 year periodicity in the mean horizontal ice speed and the zonal ice velocity. Changes in sea-ice velocity at this period might be interpreted as consequences of a circum-Antarctic wave-2 or wave-3 pattern (White and Peterson, 1996) or stationary oscillations (Kienzie, 2000; Yuan and Martinson, 2001). The longer periodicity identified here should, however, be treated with caution, as the current SSM/I time series is only long enough to resolve periodicities up to 8.5 years.

## CONCLUSIONS

We have presented an analysis of Antarctic sea-ice velocity derived from passive microwave data from the SSM/I sensor for 1988–2004. There is little evidence for a net change in annual or winter ice speed during the SSM/I record, although interannual variability is close to 30% of the velocity magnitude. Ice speeds are seasonally stratified, with lowest speeds during summer, increasing during autumn and peaking during winter and spring. For the 1998–2004 SSM/I record, June–November ice speed exceeds the annual mean speed by about 20%. Interannual variability is of similar magnitude. No net trend has been derived over the 17 year



record, although Fourier analysis indicated that mean ice speeds wax and wane with an 8.2 year period

Changes in the regional distribution of sea-ice velocity pertain to changes in the pattern of ice concentration, extent and duration, and relate to changes in the external forcing mechanisms. The regional response to changes in the atmospheric forcing, as expressed by the SAM index, appears to depend on the sea-level pressure distribution, with the ice speeding up (slowing down) on the upstream (downstream) side of the three quasi-stationary Antarctic low-pressure centres. This hypothesis may be tested by extending the SSM/I ice-motion dataset back in time. In support of this, SMMR ice-motion data are currently being reprocessed.

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