Aspects of the Ecology of Weddell seals *Leptonychotes weddellii* Along the Mawson Coastline, East Antarctica

by

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Statement of Originality

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Abstract

This study investigated the diet and patterns in occurrence of haul-out sites of Weddell seals along the Mawson coast of East Antarctica.

Scats of Weddell seals (n = 303) were collected from 139 seal haul-out sites along 250 km of coast between Fold Island (Kemp Land coast – 66.83°S, 58.79°E) and Auster Islands (MacRobertson Land coast - 67°25'S, 63°50'E) during 1998 to 2000. Identification of species-specific hard parts from the scats found eighteen species of fish, two species of octopod, two species of squid, and four species of crustaceans. Randomisation analyses were used to determine associations between abundance of primary prey species and year, season, geographic location and water depth at the sample collection site. No significant interannual variation was found, but the diet varied seasonally, as the squid *Psychroteuthis glacialis* featured more in the diet in the early summer months compared to winter. Larger beaks of this squid were found in scats collected from ice over deeper waters. The diet of Weddell seals along the Mawson coast is therefore more diverse than reported for other parts of Antarctica and the diet also varies seasonally and with changing bathymetry. The diversity in diet may be attributed to the complex seafloor topography along the coast, allowing seals to forage within a wide range of habitats at different depths.

For the investigation into patterns in occurrence of haul-out sites, three study areas were established in 2000 at different locations along the Mawson coast. One study area (Macey) had a high concentration of icebergs and islands, another area (Mawson) had islands near the coast and fewer icebergs, and the third area (Colbeck) had very few icebergs and no islands. Within each study area, there were two transects (1500m wide, 1500m apart) extending 20km north over the sea ice from the coast. Each study area was surveyed three times - in winter (late July), late winter (mid September) and spring (mid-October). Non-parametric tests were used to examine variation in density of haul-out sites and density of seals with respect to distance to coast, between areas and between survey periods. During the 3 surveys, 349 seals were observed amongst 165 sites across

all 3 areas. Friedman tests found no significant association of number of seal sites or number of seals with distance to coast. Kruskall-Wallis tests found significant variation between the three areas within each survey period; Macey consistently had more sites than the other two areas. Friedman tests tested for temporal variation within each area, however no significant changes in number of seal sites or number of individual seals were detected. Although not formally tested due to small sample sizes, there appeared to be no spatial separation of sexes. Weddell seal holes were also used by emperor penguins in the Macey and Colbeck areas and by crabeater seals in the Macey area.

This study implies that haul-out sites are not randomly distributed at the local scale (with differences shown between different areas along the coast, ie, regional scale) and that number of sites and number of seals hauled out on ice or seen in holes increases from winter into the breeding season. The results suggest that density of seal sites in the fast ice areas off the MacRobertson Land coast is affected by environmental factors such as bathymetry and presence of icebergs.

This study suggests that local bathymetric features have an important influence on the biology of Weddell seals in the Mawson area. Changing bathymetry is associated with variation in diet. Water depth can also influence grounding of icebergs and ocean currents that affect the physical structure and cracking of the sea ice, enabling Weddell seals to access the ice surface to breathe and to haul-out for resting and pupping.

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Chapter 1: General Introduction

Weddell seals are higher-order, air-breathing, marine predators and an unknown proportion of individuals reside throughout the year in the fast-ice regions of Antarctica. The ecology of these Weddell seals is therefore intimately linked to the fast-ice and the seafloor topography. The ice cover affects the productivity of the underlying water column through sediment fallout (Eicken 1992) and variable sea depths provide seals with a range of habitats in which to forage. Seafloor topography forces water movements which creates pressure points where fast-ice fractures, providing seals with access to the air for breathing and to the ice surface for resting and pupping.

The presence of sea ice profoundly influences the marine environment in Antarctica. Sea ice provides the productivity engine for the ice-affected regions (covering 20 x 10^6 km^2 of waters surrounding Antarctica during winter from 4 x 10^6 km^2 in summer) of the Southern Ocean (McMinn 2003). The Antarctic marine food web begins with ice algae that cling to the underside of the ice pack all winter and are transported into brine channels throughout the ice layer (Hempel 1991, Eicken 1992, Tynan 1998). As the ice melts, a phytoplankton bloom develops in the water directly beneath the ice, providing food for krill and other zooplankton, which in turn provide the main food source for higher trophic levels (Tynan and DeMaster 1997, McMinn 2003). Benthic communities that feed on particles settling out of the water column are also affected by the ice cover; the benthos receives little to no sedimentation of organic material during winter and then experiences a massive input of organic matter as the ice melts and the phytoplankton bloom occurs (Hempel 1991, Eicken 1992).

The sea-ice region of Antarctica can be divided into zones, each with distinctly different characteristics (Worby et al. 1998). Landfast sea ice, or fast-ice, is the relatively immobile zone of sea-ice adjacent to the coastline (Flato and Brown 1996). Fast-ice is immobile in that it is attached to the land and held in place by offshore islands, and is not subject to drift as the pack-ice region is (Worby et al. 1998).

The fast-ice in different sectors around Antarctica exhibits significantly different characteristics (Worby et al. 1998). These differences are partly as a result of variation in seafloor topography at different regions around the coast and this variation directly influences water movements such as upwelling and horizontal current flow (Heil et al. 1996). Though immobile, fast-ice is not unbreakable, and when tidal movements or oceanic swell penetration occur, seafloor topography defines the pressure points where fractures in the fast-ice will occur. These cracks, as a rule, take off near the protruding seaward capes, sea-bottom elevations, near islands and also between the islands. Icebergs grounded on the seafloor act as islands and tide cracks form around and between them.

In this thesis, I investigated two separate aspects of the ecology of Weddell seals: diet and haul-out site distribution. Understanding these aspects is fundamental for defining the ecological niche of Weddell seals, ie, where they sit in trophic webs and interactions with other species. Such information contributes to understanding the basic relationships between the dynamics of Antarctic marine biological populations and changes in the physical environment, which will be critical for predicting the regional effects of climate change (Nicol et al. 2000).

The region of interest for this study was the Mawson area of the East Antarctic coastline, a site where Weddell seals had not been studied before. Though previous studies have included samples (stomach contents and scats of Weddell seals) collected in the area (eg, Green and Burton 1987, Lake et al. 2003), this was the first study examining Weddell seals *in situ*. Given the local variations in topography around the Antarctic coastline, it is important to conduct studies at a variety of locations, rather than making generalisations about the ecology of seals from just one area.

Mawson (67°36'S, 62°52'E), on the MacRobertson Land coastline in East Antarctica, is a very different site compared to the other locations where most Weddell seal research has been conducted. It differs in its coastal topography and its sea ice in comparison to McMurdo Sound (77°30'S, 165°00'E) and the Vestfold Hills in Prydz Bay (68°35'S, 77°58'E), both areas where long-term Weddell seal research programs have occurred

(Testa and Siniff 1987, Green et al. 1995). Mawson is on a relatively open coastline, with no large embayments that could create gyres in the coastal seas. A few clusters of islands within 20 km of the coast help hold the fast-ice in place until very late in the summer. The fast-ice is extensive and in the year 2000 it extended more than 90 km from the coastal ice cliffs. The coastal waters at Mawson are much deeper than at the Vestfold Hills (hundreds of metres compared to tens of meters), and while the main current flow is westwards, deep submarine troughs running north-south create channels for injection of Antarctic bottom water to the coast from the continental shelf break (Heil et al. 1996). Mawson is also at lower latitude than McMurdo or the Vestfold Hills. Latitude affects the timing of the breeding season of the Weddell seals (Siniff 1991), with pupping starting in early October at Mawson, compared to mid-October in the Vestfold Hills (S. Lake, personal communication) and late October/early November in McMurdo Sound (Siniff 1991).

The aim of this thesis is to describe two aspects of the ecology of Weddell seals, diet and patterns in occurrence of haul-out sites, and investigate how they relate to physical characteristics such as bathymetry of the local region. The first objective was to identify the suite of prey consumed by Weddell seals in the Mawson area and then to determine the temporal and spatial variation in the abundance of prey species of Weddell seals. The second objective was to conduct preliminary surveys for haul-out sites over the fast-ice to elucidate patterns in haul-out site occurrence of Weddell seals in winter and early summer.

This chapter sets the stage for the chapters that follow and includes a brief description of the biology of the Weddell seal and an outline of the thesis structure. A systematic review of the literature will not be included in this introduction as the relevant literature is cited extensively in the appropriate sections.

1.1 Biology of Weddell Seals

Weddell seals have a circumpolar breeding distribution, occurring as far south as McMurdo Sound and as far north as South Georgia Island (54.5° S, 37° W). In 1958, Scheffer estimated the total population of Weddell seals to be between 200,000 and 500,000. However, Laws (1953) estimated 800,000 seals in the Antarctic Peninsula area alone and Stirling (1969a) estimated the population in the Western Ross Sea to be about 50,000. No systematic census has been conducted to determine the true world-wide population size, though currently it is reported to be stable with approximately 800,000 seals (Siniff 1991). Though the species is widespread around coastal Antarctica, sub-populations are subject to local environmental variation. Therefore multiple censuses need to be conducted at many different sites, rather than generalising total population size from one site.

Underwater vocalisation studies and genetics studies suggest that sub-populations are reproductively isolated from one another (Davis et al. 2000, Abgrall et al. 2003). Females return annually to the same pupping site, whilst young animals disperse away from their birth colonies and probably spend the first four to five years of their lives in the pack-ice regions (Siniff 1991).

Weddell seals are amongst the deepest divers and largest of the seals (leopard and elephant seals are larger, and elephant seals dive deeper than Weddell seals), with adults generally measuring about 3m and weighing 400-450 kg in early spring (Kooyman 1981). Females are slightly larger than males (Stirling 1971b). They can dive deeper than 720 m (Testa 1994) and the maximum measured time of submersion is 73 minutes (Kooyman 1981). The diving capability of Weddell seals means they can feed in benthic habitats even in quite deep waters.

The dentition of Weddell seals allows them to ream the ice around holes in order to make them larger so they can get their head through or fully haul out onto the ice. Rather than creating a new hole through thick fast-ice (over 1.5m thick at Mawson in August 2000;

P. Heil, personal communication) they break through thin ice in tide cracks by hitting the ice with their head, then use their teeth to make the hole bigger. The incisors and canines are very robust and project forwards, and the snout is small and narrow (Kooyman 1981). When seals reach a hole they blow hard out of their nostrils to clear the hole of ice crystals. The steam from the seals' breath creates a hummock of ice around the hole, making them easy to detect for observers on the surface. Ice-reaming behaviour has been observed in pups at about 6 weeks old (personal observation), however whether this behaviour is instinctive or learned from the mother is not known.

Copulation and conception occur mainly in December but implantation of the blastocyst (fertilised egg) is delayed until mid-January to mid-February. Foetal development progresses during the winter to result in birth in October (Bertram 1940). After giving birth to a single pup (Stirling 1971a), females stay with their pup constantly for about 2 weeks. The female then spends increasingly more time in the water, to mate and perhaps to thermoregulate and feed (Thomas and DeMaster 1983). Pups are generally weaned within 50 days of birth. At 6-7 wks old pups can remain submerged for 5 minutes and dive to 100m (Kooyman 1981). Pups weigh approximately 25 kg at birth, and over 100 kg by the time they are weaned (Bertram 1940).

1.2 Thesis structure

This thesis reports on two separate aspects of Weddell seal ecology. Chapter 2 is an investigation into variation of diet of Weddell seals at different temporal and spatial scales. Chapter 3 details the findings of surveys conducted over the fast ice to elucidate patterns in haul-out site density. General conclusions are then discussed in Chapter 4.

Collecting Weddell seal scats in Kista Strait

Chapter 2: Variation in the diet of Weddell seals along the Mawson coast, East Antarctica

2.1 Introduction

Knowing what Weddell seals (*Leptonychotes weddellii*) eat and how their diet varies over space and time is of fundamental importance in understanding how the species interacts with its environment. Weddell seals are one of few high-level predators foraging in the Antarctic coastal ecosystems and are the only mammal species to over-winter in the fast ice regions of Antarctica.

Large-scale spatial variation in the diet of Weddell seals has been reported (Lake et al. 2003). In McMurdo Sound, Antarctic silverfish (*Pleuragramma antarcticum*) makes up the bulk of the seals' diet, along with small fish belonging to the genus *Trematomus* (Burns et al. 1998). Along the coastline of the Vestfold Hills, seals prey upon prawns, *P. antarcticum* and a variety of mysids and benthic fish (Green and Burton 1987, Lake et al. 2003). In the Weddell Sea, the fishes *Chionodraco myersi* and *P. antarcticum* and squid are the most important prey species of Weddell seals (Plötz et al. 1991, Plötz et al. 2001).

Seasonal variation in Weddell seal diet has been reported at the Vestfold Hills, with seals switching from eating prawns and benthic fish in the austral summer to pelagic fish and squid in the winter (Green and Burton 1987). There also appears to be interannual variation in seal diet in the Weddell Sea region, with *P. antarcticum* the predominant prey in 1983 and 1985, but *C. myersi* dominating in 1986 (Plötz 1986, Plötz et al. 1991).

Seasonal variation has also been previously reported at Mawson, based on scats collected along the Mawson coast during the austral winters of 1996 and 1997, seal diet varied seasonally (Lake et al. 2003). However, that study found no spatial variation between scats collected from different areas along the coast within each year. Preliminary work with satellite telemetry has indicated that some Weddell seals forage within a confined range during winter (Testa 1994, Lake et al. 2005a). The waters along the Mawson coastline show some dramatic variation in depth with a trough descending to >500m north of Mawson and a large submerged shelf, the Storegg Bank, to the east of Mawson that is around 100 m deep. Given the potentially limited foraging range of Weddell seals at least during winter and even more so during the summer for breeding seals, any variation in the diet between sites might be associated with variable water depths in this area.

The main objectives of this study were 1) to identify the species consumed by seals within the study area, 2) to determine if the diet of Weddell seals varied seasonally and interannually, and 3) to determine if any spatial variation was associated with depth or coastal location.

2.2 Materials and Methods

2.2.1 Study area

The study area included portions of the MacRobertson Land and Kemp Land coasts up to 200 km west and 60km east of Mawson Station (67°36'S, 62°52'E). The coastline where scats were collected was divided into zones that incorporated the major island groups along the coast, which are roughly 50 km apart. Zone 1 includes the Robinson Group of islands, the Auster Islands, and further eastwards; Zone 2 includes the islands surrounding Mawson Station; Zone 3 incorporates the Stanton Group; and Zone 4 includes the Colbeck Archipelago and further west (see Figure 2.1). Depth classes were taken from a map of the Mawson coastline obtained from the Antarctic Division Data Centre (Figure 2.1). Depth class 1 incorporated depths 0-100 m, class 2 100-250 m, class 3250-450 m, class 4 450-1000 m and class 5 included depths 1000-2500 m. A sixth class included those samples that were collected at sites where there is no available depth information, these samples were not included in any analysis comparing scat composition between different depth classes.

2.2.2 Collection of samples

A total of 303 scats were collected from 139 sites along the MacRobertson Land and Kemp Land coast over three summer periods and three winter periods from January 1998 to November 2000 (Table 2.1). Summer included the months October to March when the seals are pupping, mating and moulting. Winter included the months April to September, and covered the time of maximum sea-ice extent and the darkest time of the year when biological productivity is at its lowest (El-Sayed 1971, Eicken 1992).

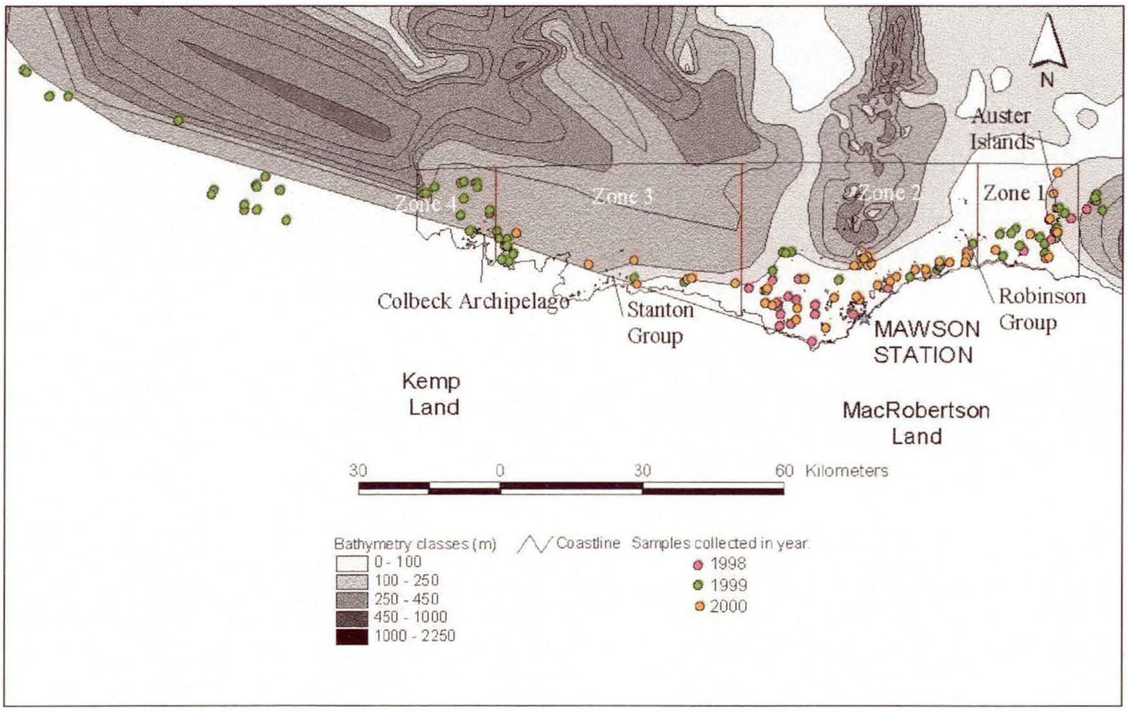


Figure 2.1 Map of the Mawson coastline showing the sites of sample collection in the three years of the study. The map also includes the study zones along the coast (note, zones 1 and 4 extend eastwards and westwards respectively) and shows the bathymetry as is currently available from the Australian Antarctic Division Data Centre.

Table 2.1 Number of samples collected and period of collection in each year.

Year	Collection period	Season	Number of samples
1998	January to October	Summer	9
		Winter	17
1999	May to September	Winter	139
2000	May to November	Summer	45
		Winter	93

In all years, scats were collected during the period of safe ice travel for vehicles. Seal haul-out sites (holes through the ice where the seals accessed the ice surface for resting) were sighted whilst driving over the sea ice, and scats were collected from the ice surrounding these sites. Only Weddell seals and emperor penguins (*Aptenodytes forsteri*) used these holes during winter, and the scats left by Weddell seals were easily distinguished from those left by emperor penguins by their colour, volume, consistency, and scent.

Scats were extracted from the ice in their entirety by digging and/or chipping with a shovel and ice-axe, and placing the whole sample into a labelled bag. Due to limited storage space at the station, maximally one fifth and minimally one of the available scats were collected at a site. The remaining scats were chipped up and destroyed so that old scats were not collected during subsequent visits to the site.

2.2.3 Processing of scats

Scats were placed in separate 4um mesh bags with waterproof labels. Up to 8 bags were placed in a washing machine and the samples were allowed to thaw in the water before the washing machine was started on a regular wash cycle which was allowed to continue for 10 minutes. This broke up the samples, separated flesh from the hard parts and removed the flocculent material.

After washing, the bags were removed one-by-one from the washing machine, rinsed in cleaned water, turned inside out and the contents of the bag hosed into a large tray. The tray was then emptied into a sieve (250 μm pore size) to remove the rocky dirt, and the remains then tipped into a shallow, black, circular sorting dish. Black was found to be the best colour for the dish (white and green dishes were also tried) because otoliths showed up virtually luminescent against the black when under a light source.

Hard parts were removed and fish vertebrae and jaw bones, cephalopod beaks and crustacean carapaces were separated and stored in 70% ethanol. Fish otoliths were stored dry in plastic bags. The presence of seaweed, sand and stones was noted, as well as a count of the number of nematodes in the sample. The retained hard parts were then examined under a dissecting microscope and identified to the lowest taxonomic level.

Otoliths were identified using Williams and McEldowney (1990). Otoliths were classified on a scale of an scale of 1-5: 1 being a rounded disc with absolutely no distinguishing features, and 5 being a perfectly intact otolith (there were no "5s" obtained, but we had "perfect otoliths" to compare them to in Williams and McEldowney, 1990). Otoliths with a classification of 3 or above were measured (length and width) using digital analysis software (Optimas 6) and determined as coming from the left or right side. Number of fish per sample was calculated by counting all otoliths per left or right side per sample, then determining that the side with the most otoliths equalled the minimum number of fish.

Cephalopod beaks were divided into upper and lower beaks, and lower beaks were used for identification. Number of individuals per sample was based on the number of lower beaks. Identification of squid lower beaks was based on Clarke (1986) and by comparing with beaks in collections at the University of Tasmania. Octopus beaks were compared with Daly and Rodhouse (1994), Lu and Stranks (1994) and Allcock et al. (2001). Lower rostral lengths (LRL) and crest lengths were measured on squid and octopus beaks that were not too chipped or broken. Prawn identification was determined using Kirkwood (1984); amphipods and isopods were identified using O'Sullivan and Hosie (1985).

2.2.4 Data Analysis

Relative frequency of occurrence (%FOO) was determined as a measure of the rate at which prey types were targeted and the number of individuals of each species was recorded (when possible) for additional information about the relative proportions of prey in the diet (Lake et al. 2003). Statistical analyses were based on matrices of abundance of each prey species per scat. The dependent variable was the abundance of prey species within each sample, and independent variables were year, season, coastal zone and water depth. Due to the unbalanced sample design, these variables were combined in several different tests in an effort to reduce variation (see Table 2.2).

Table 2.2 Combinations of the independent variables tested by randomisation analysis. These combinations were put together to test for temporal and spatial variation, minimising the error introduced by the unbalanced sample design.

Test	Years	Seasons	Zones	Depths	n
i	1999	winter	1, 2, 3, 4	1, 2, 3, 4	139
ii	2000	summer, winter	1, 2, 3	1, 2, 3	138
iii	1998, 1999	winter	1	1, 2, 3	17, 139
iv	1999, 2000	winter	2, 3	1, 2, 3	139, 93
v	1998, 2000	summer, winter	1, 2	1	9, 17, 45, 93
vi	1998, 1999, 2000	winter	1, 2	1	17, 139, 93

Diet composition was compared using randomization methods (Manly 1997; S. Wotherspoon, personal communication). Multi-variate analysis of variance (MANOVA) was used to test for interactions between the main effects (Sokal and Rohlf 1995, George and Mallery 2001). All means are given ±1SD; significance levels were set at p=0.05 unless stated otherwise.

To reduce the number of zeros in the analysis, species that occurred in less than 5% of the cumulative FOO were not included in the MANOVA or randomisation analyses. This removed the rarer species whilst retaining at least one species from each of the prey orders that were represented.

Randomisation tests were performed because they are non-parametric and make no assumptions about the data's distribution (Manly, 1997). However, they do not test for interaction effects (S. Wotherspoon, personal communication). Randomisation tests bound the columns (prey species) while randomising the rows (see Lake et al. 2003). Two-way randomisation tests were conducted as separate one-way analyses, where one factor was held constant (eg, season) while the other factor (eg, zone) was randomised, and vice versa. Under the null hypothesis, the randomised factor was not significant in determining the diet. The steps to randomisation 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 were true, then the observed value of F is within the distribution of 95% of the Fs calculated from random allocation (Lake et al. 2003).

2.3 Results

2.3.1 Diet composition

From the 303 Weddell seal scats collected, 235 had identifiable prey remains and 3082 identifiable prey items were recovered. *Pleuragramma antarcticum* was the most abundant species with at least 1575 individuals recovered from scats and also the most frequently occurring (43.9 % FOO) prey species across the entire collection of Weddell seal scats (see Table 2.3). The next most frequent species were the octopus *Pareledone* sp. 1 (27.7 % FOO), gammarid amphipods (17.8 % FOO), the notothen *Trematomus newnesi* (16.8 % FOO), the squid *Psychroteuthis glacialis* (7.6 % FOO) and the prawn *Chorismus antarcticus* (5.0 % FOO). At least 21 other species were identified but did not occur in more than 5 % of all samples. Sixty-seven of the 303 scats (22.1 % FOO) contained sand, and 93 scats (30.7 % FOO) contained stones. Many scats (85.5 % FOO) contained large numbers of nematode worms. These were not identified further nor included in statistical analyses as they are internal parasites either in the seals' gastro-intestinal tract or in that of their prey, and are not prey items.

The size frequency distributions of the primary prey species with measurable hard parts (otoliths or beaks) are shown in Figure 2.2. Otolith lengths and lower rostral lengths of squid were converted into body lengths using equations in Williams and McEldowney (1990) and Groger et al. (2000). The mean length of *P. antarcticum* individuals retrieved from scats was 105.55 mm ± 11.92, and the mean length of *T. newnesi* individuals was 131.40 mm ± 25.80. The mean mantle length of *P. glacialis* across all samples was 210.21 mm ± 77.06.

Table 2.3 Diet of Weddell seals described by frequency of occurrence (% FOO), minimum number of individuals and relative number of individuals (% of identifiable individuals excluding nematodes) of each species extracted from the 303 Weddell seal scats collected in 1998, 1999 and 2000.

Prey species	Habitat	% FOO	# of individuals	relative number (%)
Fish		**55.78**		
Pleuragramma antarcticum *	pelagic; 0-800m †	43.89	1575	51.10
Dissostichus mawsoni	bentho-pelagic; shelf and upper slope; 100-1600m ‡	0.33	1	0.03
Trematomus bernacchi	inshore benthic; sublittoral to 700m, though not over the continental shelf and most commonly in upper 200m* †,‡	3.30	16	0.52
T. borchgrevinki	cryopelagic (under-surface of sea ice); 0-50m †	0.33	1	0.03
T. centronotus	benthic; inshore to 680m †	0.33	3	0.10
T. eulepidotus	benthic from nearshore to continental shelf; mostly 100-500m †,‡	0.66	2	0.06
T. hansoni	nearshore benthic; 20-100m, though can occur to 550m †,‡	0.33	1	0.03
T. loennbergi	bentho-pelagic; 65-832m, mostly at depths > 300m †,‡	0.33	2	0.06
T. newnesi *	benthic; 0-400m †,‡	16.83	191	6.20
T. nicolai	benthic; 0-420m †,‡	0.99	3	0.10
T. scotti	benthic from nearshore to continental shelf; 20-793m †,‡	0.66	2	0.06
Trematomus sp.		5.61	26	0.84
Chaenodraco wilsoni	bentho-pelagic on continental shelf; 300-450m †	1.32	7	0.23
Chionodraco hamatus	benthic; 4-600m †,‡	0.66	2	0.06
Chionodraco myersi	benthic; 200-800m †,‡	0.33	2	0.06
C. wilsoni sub-group		2.64	8	0.26
Dacodraco hunteri	bentho-pelagic; 350-850m†	0.33	1	0.03
Pagetopsis macropterus	bentho-pelagic; 5-655m †,‡	0.33	1	0.06
Prionodraco evansii	benthic;70-550, mostly above 450m †,‡	0.33	1	0.03
Vomeridens infuscipinnis	deeper waters of continental shelf; 419-813m †,‡	0.33	1	0.03
unidentified fish/ otoliths too eroded		33.33		
Cephalopods		**43.89**		
Pareledone sp 1. *	benthic over continental shelf; 25-680m ¥	27.72	396	12.85
Pareledone sp 2.	benthic over continental shelf; 25-680m ¥	1.65	7	0.23
unidentified octopus		3.96	16	0.52
*Psychroteuthis glacialis**		7.59	44	1.43
Gonatus antarcticus		0.33	1	0.03
unidentified squid		1.65	5	0.16
Crustaceans		**42.57**		
Chorismus antarcticus *	inshore benthic; 15-300m §	5.00	22	0.71
Notocrangon antarcticus	demersal; 15-1320m, mostly 300-600m §	3.30	15	0.49
unidentified prawns				
Mysida £		1.32		
Gammarid amphipods £ *		17.82	133	4.32
Hyperiid amphipods £		1.98	7	0.23
Poriferans	benthic	3.96		
Nematodes	GIT parasite	85.48	>6500	

References † Williams and McEldowney, 1990
‡ Gon and Heemstra, 1990
§ Kirkwood, 1984
£ O'Sullivan and Hosie, 1985
¥ Lu and Stranks, 1994

* prey species included in statistical analysis

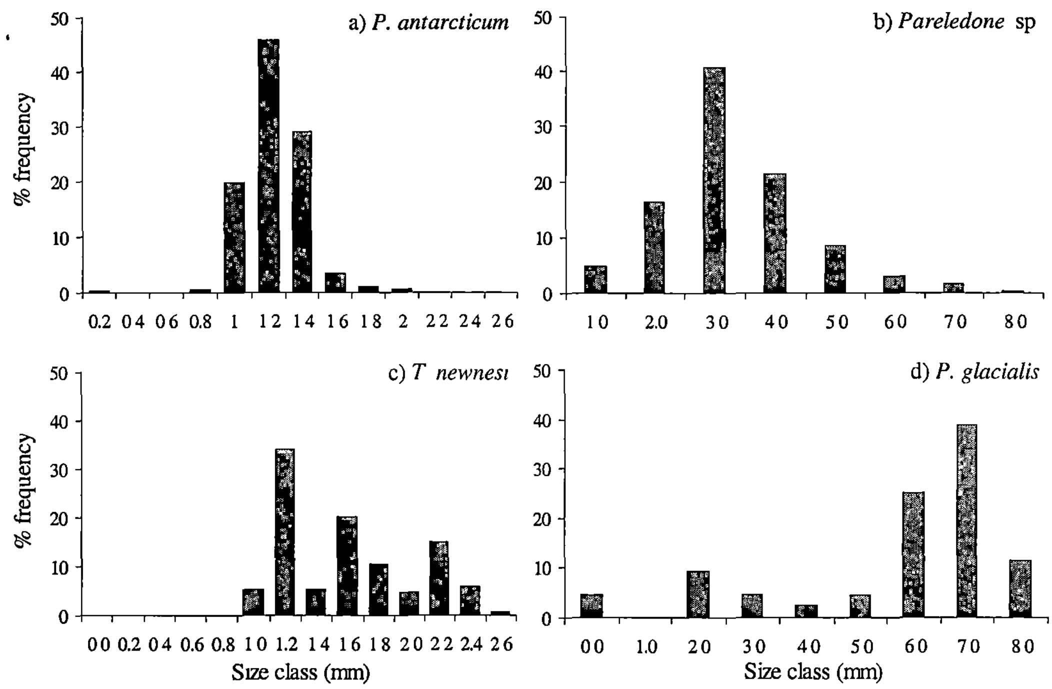


Figure 2.2 Standard length frequency distributions of otoliths and cephalopod beaks of primary prey species across all samples.

2.3.2 *Interannual variation*

A comparison of all three years (test *vi*, see Table 2.2) showed no significant variation in abundance of primary prey species between the years ($F_{12, 106} = 0.901$, $p = 0.530$). Also, the abundance of primary prey species was compared between 1998 and 1999 (test *iii*), and 1998 and 2000 (test *v*) and showed no significant variation. However, dropping data from 1998 from the analysis and comparing diets from 1999 and 2000 (test *iv*) showed significant variation in the abundance of all primary prey species combined between the two years ($F_{6, 109} = 0.893$, $p = 0.044$), influenced by gammarid amphipods ($F_{6, 109} = 5.527$, $p = 0.019$). The mean number of gammarids per scat in 1999 was 0.15 ± 0.51 ($n = 33$) and in 2000 it was 1.10 ± 2.30 ($n = 77$).

2.3.3 *Seasonal Variation*

Comparisons were made within the year 2000 (test *ii*), and combining the data for 1998 and 2000 (test *v*). Within the year 2000, seasonal variation in the abundance of prey items was significant ($F_{6, 136} = 0.903$, $p = 0.025$). The squid *P. glacialis* accounted for most of the variation ($F_{6, 136} = 9.147$, $p = 0.002$). The mean number of *P. glacialis* individuals per scat was 0.27 ± 0.75 (n = 45, 15 %FOO) in summer and 0.020 ± 0.146 (n = 93, 2 %FOO) in winter.

With the 1998 and 2000 data combined (test *v*), there was no variation across the prey species overall ($F_{6, 104} = 0.912$, $p = 0.149$), yet *P. glacialis* varied significantly ($F_{6, 104} = 6.555$, $p = 0.021$) when the species were tested individually. No other species showed a seasonal pattern in their abundance in the scats.

A size frequency histogram for *P. glacialis* shows a bimodal distribution of lower rostral lengths across all samples (see Figure 2.2d). The larger size classes (6.01-8.00mm LRL) were more abundant than the smaller sizes (2.01-3.00mm LRL). It was found that the larger squid occurred mostly in September and the smaller sized squid occurred mostly in August. *P. glacialis* individuals from scats collected in September (mean = 253.64mm ± 48.52, n = 22) were significantly larger than those from August (mean = 171.72 mm ± 57.84, n = 6; F = 12.43, p = 0.002), though the results must be treated with caution given the unequal sample sizes.

2.3.4 Variation along the coast

Tests *i* and *ii* compared all of the zones (1-4 and 1-3 respectively) within different years (1999 and 2000 respectively), and tests *iv* and *vi* compared zones 2 and 3, and zones 1 and 2 respectively.

Randomisation results for test *i* showed significant variation in abundance of prey species between all of the zones ($F_{18, 138} = 0.645$, $p = 0.004$), influenced mainly by *Pareledone* sp. 1 ($F_{11, 138} = 3.845$, $p = 0.01$). *Pareledone* sp. 1 was most abundant in zone 2 (mean = 1.08 ± 2.95 individuals/scat, n = 24), and least abundant in zone 4 (mean = 0.17 ± .069 individuals/scat, n = 4).

Randomisation showed no significant variation between the zones ($F_{12, 136} = 0.868$, $p = 0.108$). MANOVA reported a significant interaction effect between depth and zone on the abundance of *P. glacialis* individuals in scats ($F_{2, 240} = 5.601$, $p = 0.005$). *P. glacialis* individuals were more abundant in zone 3 (mean = 0.330 individuals/scat ± 1.047, n = 15) and did not occur in any samples in zone 1 (n = 25).

Comparison between zones 1 and 2 across all years of the study (test *vi*) showed no significant difference in abundance of primary prey species ($F_{6, 109} = 0.799$, $p = 0.101$). Also, there was no significant difference between zones 2 and 3 when data from years 1999 and 2000 was combined (test *iv*; $F_{8, 109} = 0.920$, $p = 0.211$).

2.3.5 *Effect of bathymetry*

Comparison between bathymetry classes 1 to 4, across all of the zones within 1999 (test *i*, see Table 2.2), showed there was significant variation in the abundance of individuals of the primary prey species ($F_{24, 138} = 0.727$, $p = 0.029$). Individual tests of the primary prey species showed significant variation in the abundance of *P. glacialis* individuals between different depth classes ($F_{24, 138} = 4.990$, $p = 0.011$). *P. glacialis* was most abundant in samples collected over depths between 450 and 1000m (depth class 4, mean = 1.830 individuals/scat ± 4.021, n = 6) and occurred least in samples collected over depths between 100 and 250m (depth class 2, mean = 0.060 individuals/scat ± 0.250, n = 16). There was no significant interaction effect between depth and zone in this test ($F_{30, 466} = 1.387$, $p = 0.086$).

Test *iv* (see Table 2.2) revealed no significant variation in abundance of all primary prey species between depth classes ($F_{12, 109} = 0.799$, $p = 0.101$), but there was significant variation in the abundance of *P. glacialis* individuals between different depth classes ($F_{12, 109} = 9.543$, $p = 0.028$). In this case, *P. glacialis* individuals occurred most abundantly in samples collected from ice over depths between 250 and 450m (depth class 3, mean = 0.600 individuals/scat ± 1.342, n = 5). *P. glacialis* individuals had a low level of abundance in waters 0-100m deep (depth class 1, mean = 0.030 individuals/scat ± 0.168, n = 70), and did not occur in any samples collected over waters of 100-250m depth (n = 36).

Comparisons of mantle lengths of *P. glacialis* individuals by ANOVA showed significant variation ($F = 5.41$, $p = 0.002$, $df = 4$, $n = 37$) between depths, with *P. glacialis* collected over waters between 0 and 100m deep averaging 153.79mm ± 78.14 (n = 16) and those collected over waters 450-1000m deep averaging 264.39mm ± 40.89 (n = 11).

2.4 Discussion

2.4.1 Diet composition

The diet of Weddell seals along the Mawson coastline was variable over both space and time. In this area, the seals consumed a wider range of fish and invertebrate species (see Table 2.3), with 27 species of prey (18 fish, 4 cephalopods and 5 crustaceans identified from 303 scats) as compared to 18 species (13 fish, 2 cephalopods and 3 crustaceans from 586 scats) from an equivalent study at the Vestfold Hills area (68°35'S, 77°58'E) (Lake et al. 2003). This suggests that the prey fauna is more diverse along the deeper waters of the Mawson coast compared to the shallower waters off the Vestfold Hills.

As found in previous studies, Antarctic silverfish was found to be the most important prey species in the diet of Weddell seals at Mawson (Green and Burton 1987, Lake et al. 2003). The importance of *P. antarcticum* in the High-Antarctic Zone has been compared to that of *Euphausia superba* in the Seasonal Pack-Ice Zone (Kock 1992). It is described as the dominant pelagic fish of the shelf waters around the Antarctic continent (Gon and Heemstra 1990) and is a major constituent of the diet of virtually every large predator feeding over the East Antarctic continental shelf (Williams and McEldowney 1990). Emperor penguins (*Aptenodytes forsteri*) and Adélie penguins (*Pygoscelis adeliae*), which both occur in large breeding colonies along the Mawson coast, also include *P. antarcticum* in their diet (Robertson 1995, Wienecke and Robertson 1997, J. Clarke, personal communication). However, inter-specific competition is minimized by temporal and geographic differences in foraging habitats (Wienecke and Robertson 1997, Clarke et al. 1998, Burns and Kooyman 2001), as well as by different prey preferences: emperor penguins take more squid and Adélie penguins take more krill (Robertson 1995, Clarke et al. 1998). Satellite telemetry studies have shown that Emperor penguins and female

Adélie penguins forage in the pack-ice over the continental shelf edge (Wienecke and Robertson 1997, Clarke et al. 1998). Weddell seals tend to prefer foraging under fast-ice and heavy pack-ice within 50-100 km of their summer breeding colonies (Testa 1994). Differences in breeding chronology of the three species also means that the penguin and seal populations are concentrated at different times and therefore the local predation pressure may be spread throughout the year. The potential issue of competition between Weddell seals and the penguins affecting the survival of either species warrants further investigation, especially given that *P. antarcticum* was explored as a target species for a commercial fishery by Russia in the late 1980s (Kock 1992), and also because the potential for a krill fishery exists off the continental shelf north of Mawson (Clarke et al. 1998). Knowing the trophic relationships that exist in the Mawson area would assist with determining the impact of any commercial fisheries.

In terms of frequency of occurrence, the next most frequently targeted prey species in the diet of Weddell seals at Mawson were the octopod *Pareledone* sp. 1, gammarid amphipods, the fish *Trematomus newnesi*, the squid *Psychroteuthis glacialis* and the natant decapod *Chorismus antarcticus*. Remains of individuals of species that were discovered in scats collected for this study, but not in samples studied by Green and Burton (1987) or Lake et al. (2003), included the fish species *Dissostichus mawsoni*, *T. centronotus*, *T. hansoni*, *T. nicolai*, *Dacodraco hunteri*, *Pagetopsis macropterus*, *Prionodraco evansii*, *Vomeridens infuscipinnis* and the squid *Gonatus antarcticus*. *D. mawsoni* were likely underrepresented in scats because Weddell seals consume the body but discard the head (Pierce and Boyle 1991, Lake et al. 2003; R. Williams, personal communication). The species identified by Lake et al. (2003) as occurring in seal diet at Mawson, but not found in this study, included the fish *Aethotaxis mitopteryx*, *Notothenia coriiceps*, *Lepidonotothen kempi* and *T. pennelii*. Trawl sampling, such as that conducted in the Weddell Sea (Plötz 1986, Plötz et al. 1991, Plötz et al. 2001), would provide useful information to help determine if these species are regularly present in the waters off the Mawson coastline, or if they are irregular visitors, which in turn would help determine why the species are rare in the diet of Weddell seals.

Estimating the size of the fish from the lengths of otoliths found in scats reveals that the seals are feeding on *P. antarcticum* juveniles and sub-adults approaching sexual maturity (Gon and Heemstra 1990). These age classes are thought to occur in the mid-upper pelagic waters with older larger adults occurring deeper than 400m, near the bottom over the shelf (Hubold and Ekau 1987). The depths that the adults inhabit do not put them beyond the diving range of Weddell seals, however it is possible that the adults of *P. antarcticum* occurred further offshore than the foraging range of the seals that would have been sampled in this study. Additionally, Weddell seals may find more energetically profitable prey at depths >400m than *P. antarcticum*, such as octopus and larger nototheneid fish such as *T. newnesi*.

2.4.2 Interannual variation

The only significant interannual difference in the diet of Weddell seals was in the numbers of gammarid amphipods. The low sample size from 1998 (n = 13) and high standard deviations about the mean number of amphipods per sample (0.23 ± 3.00) contributed to the low power of the test comparing all three years together. However, upon removing the 1998 data, a significant difference was found between 1999 and 2000 in the number of gammarids per scat, with more amphipods occurring in 2000. The year of lower gammarid (1999) abundance in the seal diet coincided with a year of low breeding success for Adelie penguins (0.50 chicks per nest in the 1999-2000 summer, unpublished CEMP data held at Australian Antarctic Division). In the 2000-01 summer, the breeding success of the Adélie penguins was higher (0.81 chicks/nest). This increase in breeding success corresponded with an increase in the proportion of krill and a decrease in the proportion of amphipods retrieved from stomach flushing samples (Clarke 2001; unpublished CEMP data held at AAD). Thus processes acting upon krill abundance may influence gammarid abundance. In years of increased krill abundance, gammarid abundance may also increase, meaning more gammarids are available for Weddell seals to eat. However, the fluctuations in gammarid numbers may not have any effect on the Weddell seals beyond a simple lessening in the diet because the seals consume such a wide variety of other prey that they can easily make up any shortfall.

It has been proposed that the relationship between breeding success, sea-ice extent, foraging trip duration and diet for Adélie penguins is associated with the large-scale climactic processes that drive the Antarctic Circumpolar Wave (ACW; Clarke et al. 2002). White and Peterson (1996) proposed that climate and oceanography cycles around the Southern Ocean have a ~4-6 year periodicity, and it is likely that Weddell seals are also affected in some way, as the local Adélie penguin population is. Given that it is likely that whatever oceanographic processes influence timing of the fast-ice breakout would probably also affect the availability of prey in the Mawson region (Clarke et al. 2002), it is possible that diet studies need to be conducted over time periods longer than 6 years in order to determine if Weddell seal diet fluctuations are associated with the ACW.

2.4.3 Seasonal variation

It seems reasonable to expect that, of all the independent factors included in the analysis, the different seasons would explain a significant proportion of the variation in the diet of Weddell seals. This could be expected because the different seasons are associated with changes in the sea-ice which affect the productivity of the waters beneath the ice. During winter the ice gradually thickens and productivity virtually ceases; then with the onset of summer there is sub-surface erosion of the sea ice, with a subsequent complete thaw in late summer (Eicken 1992).

However, only numbers of *P. glacialis* were solely responsible for the variation in abundance of primary prey species between winter and summer, despite the relatively low %FOO compared to the other primary prey species. *P. glacialis* has a circumpolar distribution and individuals may aggregate on or near the sea floor close to the edge of the continental shelf (Lu and Williams 1994). *P. glacialis* individuals might change habitat during development, with small and young individuals living at shallow depths and larger older individuals living on or near the bottom (Jackson and Lu 1994, Lu and Williams 1994). This scheme is consistent with the pattern of the diet of Weddell seals in the present study as it was found that the remains of larger squids were found in scats collected on ice over deep water (450 - 1000m) and remains of smaller squids were found in scats collected over shallower waters (<100m).

There are several reasons for the increasing abundance and then cessation of occurrence of larger squid in the diet of seals, including changes in seal foraging distribution, depletion of squid stock by predators, or senescence of squid after a protracted spawning period in late winter or early spring (Lu and Williams 1994, Lake et al. 2003). The data from this study does not illustrate changes in the abundance of the other primary prey species (which range in habitat from benthic to pelagic in all months) in the Mawson area. Therefore it is not evident that the seals have altered their foraging patterns to exploit the squid. Moreover, diving behaviours would have to be examined concurrently with diet analysis to assess this possibility. Another possibility is that the squid migrate elsewhere and move out of the seals' foraging area. More information on the biology of *P. glacialis* would help answer this question, as it could be an energetically important prey item in the seals' diet. *P. glacialis* individuals are described as muscular squids (Fischer and Hureau 1985), typically consisting of 80% muscle (O'Dor and Webber 1986). Thus this species could provide a high energy meal for a seal, especially coming into the breeding season. It would also be useful to determine if *P. glacialis* is an even more important diet component for Weddell seals that haul out on ice further offshore than were able to be sampled in this study.

2.4.4 Spatial variation

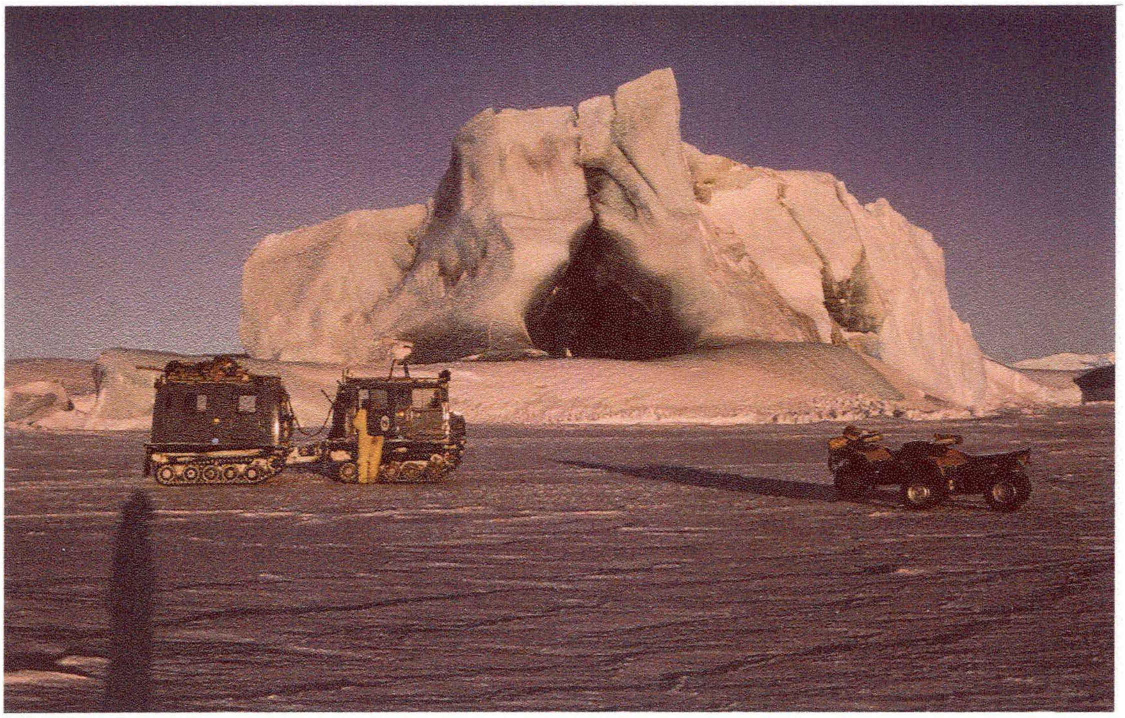
Spatial variability in diet was more influenced by bathymetry compared to longitudinal positions of scats collected along the coast. The Mawson coastal profile is relatively smooth with few inlets or promontories to disturb horizontal water flow (see Figure 2.1). Depth, on the other hand, could be expected to explain more variation, especially in the Mawson region, where dramatically different depths are available to be exploited by seals. The continental shelf off MacRobertson Land is characterised by relatively deep channels shoreward of the outer shelf break, providing access for coastal waters to the deep sea (Smith and Tréguer 1994).

The interaction between depth and zone on the abundance *of P. glacialis* in this study is not surprising, but cannot be dismissed as simply due to unbalanced sample design. The coastal zones that were arbitrarily assigned do not have an equal distribution of water depths; the water depth gradually increases as you move west and north from the Auster Islands. Most samples were collected within 20km of the coast.

P. glacialis was more abundant in scats collected at haul-out sites over deeper waters than shallow waters, and hence more abundant in the Zones 3 and 4 (characterized by deeper waters) than in Zones 1 and 2 (mostly 0-100m deep). *P. glacialis* individuals found in scats collected over deeper waters tended to be larger than those found in scats collected over shallow waters. As explained earlier, *P. glacialis* may exhibit ontogenetic shifts in habitat (Lu and Williams 1994), and this might mean that Weddell seals feed on larger adult squid in deep water and small young squid in shallow waters.

2.4.5 Conclusion

A major conclusion of this study is that the diet of Weddell seals along the Mawson coast is more diverse than reported from other parts of Antarctica. Variation between years, seasons and depths was found. Further study on competition for resources between Weddell seals, Emperor penguins and Adélie penguins is warranted. Also, investigation into the influence of environmental parameters such as the ACW and sea ice extent on Weddell seal diet variability would increase our understanding of the Antarctic marine ecosystem.



Vehicles used in seal surveys in front of a jade iceberg in the Macey area

Chapter 3: Patterns in occurrence of haul-out sites of Weddell seals along the Mawson coastline, East Antarctica

3.1 Introduction

The Weddell seal is the only mammal to over-winter and rear its young in the fast-ice regions of Antarctica. Although it is the most widely studied of the Antarctic seal species, very little work has been done regarding its association with the ice substrate under which it dives for food and upon which it rests and bears its young. Sea ice is not simply an inert covering of the ocean surface around Antarctica, covering up to 20 x 10^6 km^2 of the waters surrounding Antarctica during winter-time and receding to less than 4 x 10^6 km^2 in the austral summer (Zwally et al. 1983). Sea ice also structures Antarctic marine ecosystems because its growth, drift and decay through space and time influences the interactions between different groups of organisms and their environment (Eicken 1992). It is therefore important to understand the basic relationship between seals and sea ice in order to be able to determine the effect of variation in ice characteristics such as maximal ice extent and maximum ice thickness on the population processes of Weddell seals, such as breeding success. This is especially important given the growing concerns regarding climate change and the need to obtain baseline biological data in order to determine the effects of large-scale climatic changes on Antarctic marine ecosystems (Weimerskirch et al. 2003).

The majority of Weddell seal studies have been conducted at McMurdo Sound in the Ross Sea, the Weddell Sea and at the Vestfold Hills at the eastern edge of Prydz Bay (eg, Smith 1965, Stirling 1971a, Testa 1994, Green et al. 1995, Bester et al. 2002, Lake et al. 2005b). The sea ice in different sectors of the Antarctic coast exhibits quite different characteristics (Worby et al. 1998), which may exert different influences on local Weddell seal populations; therefore it is important that surveys are conducted at locations all around Antarctica and local associations between seals and ice be quantified. Prydz Bay, like the Weddell and Ross Sea regions, is a large embayment with cyclonic ocean currents influencing the drift and distribution of the ice in a different way to the rest of the East Antarctic region (Smith and Tréguer 1994, Worby et al. 1998). The ice along the majority of the East Antarctic coastline, such as the MacRobertson Land coastline (where Mawson station is located), consists of a narrow and highly mobile band of sea ice (Worby et al. 1998). The land-fast ice band is immobile and extends in a continuous sheet northward from the continent, with maximum ice extent at Mawson exceeding 80km offshore (Worby et al. 1998). Each year, the fast ice typically maintains a slow thermodynamic growth from March to late September, with surface ablation and bottom melt occurring before the ice breaks out between December and February (Heil et al. 1996).

Only one other study, conducted at the Vestfold Hills region in Prydz Bay (Lake et al. 2005b), has attempted to quantify the relationship between occurrences of sites where Weddell seals haul-out and environmental factors associated with fast-ice habitat. Lake et al. (2005b) hypothesized that haul-out site occurrence is associated with factors that increase the likelihood of the ice cracking, namely distance to coast and distance to fast-ice edge. Lake et al. (2005b) predicted that by surveying transects across the gradient of haul-out site distribution the point at which there is sufficient distance from the land for fast-ice to move freely could be determined.

At a finer scale, it is possible that there may be some spatial segregation between sexes or breeding/non-breeding groups. Adult females hauling out to pup prefer stable inshore fast-ice (Siniff et al. 1977), and the polygynous mating system may mean that non-breeding males are excluded from these areas (Kooyman 1981). These patterns may show up as "zones" with female only and male only sites. As no difference in ice-abrading ability between males and females has been reported, i.e., ability to create and maintain a hole through the ice, we could surmise that spatial segregation could be due to social behaviours, and may have an effect on the foraging range or areas of different components of the population.

The main aim of this study was to conduct surveys of Weddell seal haul-out sites (herein referred to as "sites") over the fast-ice along the MacRobertson Land coast east and west of Mawson Station to elucidate the patterns in distribution of hauled-out Weddell seals. In particular, the number of sites and the number of seals were compared between different areas along the coast, and also compared over time as the winter progressed into the summer breeding period. Furthermore, the sex and age composition of groups hauled out on the ice was also observed in order to determine if there was any segregation between different elements of the population. An associated aim was to determine if the results of this study support Lake et al's (2005b) hypothesis that occurrence of Weddell seal sites is associated with factors that contribute to formation of cracks in the fast ice.

3.2 Methods

3.2.1 Survey design and data collection

From July to October 2000, three fast-ice areas off the MacRobertson Land coastline were surveyed for Weddell seal sign such as scats, imprints and ice holes (see Figure 3.1). The three areas were positioned around Mawson Station (67.60°S, 62.87°E), Macey Islands (~50 km east of Mawson at 67.43°S, 63.83°E) and at the Colbeck Archipelago (~100 km west of Mawson at 67.43°S, 60.73°E). Within each area, two transects were traversed, searching for any seal sign and ice holes that serve as breathing holes or where seals can haul out onto the ice surface. A cluster of seal sign around a hole was regarded as one encounter site, as it was not possible to determine the number of seals from the sign. Small breathing holes could be distinguished from the surrounding ice by the ice mound that developed around the hole, and many sites were located by the presence of scats and/or the imprints left behind by a warm seal melting into the ice. The sex of the seal that left an imprint was inferred from the position of urine stains on the ice if visible – imprints left by females have a stain around the hind flippers, and those left by males have a stain about halfway along the abdomen.

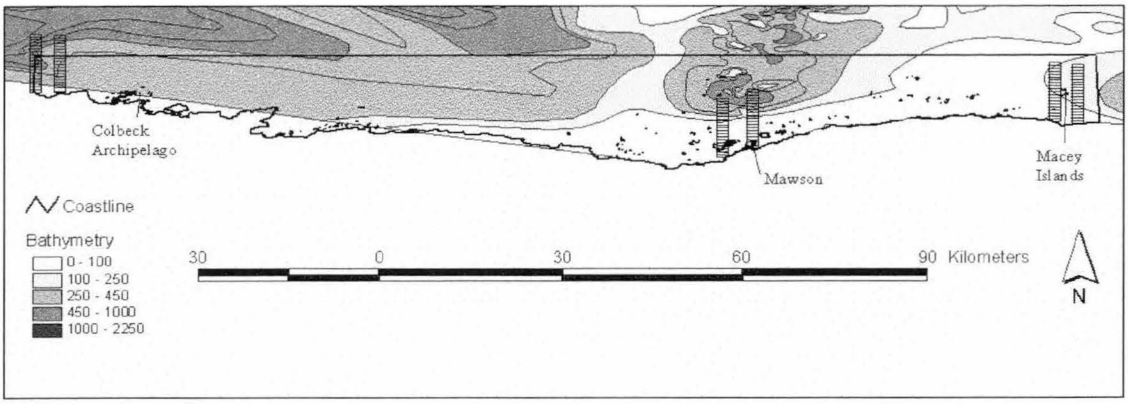


Figure 3.1 Map of Mawson coastline showing positions of transects and bathymetry.

Table 3.1 Geographic coordinates (in decimal degrees) of midpoints of the southern end of each transect.

Area	Transect	Latitude	Longitude
Mawson	1	67.6234°S	62.8080°E
	2	67.5739°S	62.8915°E
Macey	1	67.5171°S	63.7962°E
	2	67.5168°S	63.8645°E
Colbeck	1	67.4207°S	60.7081°E
	2	67.4337°S	60.7755°E

Each area was surveyed three times with transects in the same area being surveyed on the same day when possible. Survey periods were 31 July - 10 August (deep winter), 15 - 23 September (late winter) and 16 - 20 October (spring). The transects in each area were 1.5 km wide and separated by 1.5 km and extended 20 km from the coastal ice cliffs (continental edge). The coordinates for the midpoint of the southern end of each transect (t/s) are shown in Table 3.1.

Surveys were started by using a global positioning system (GPS) instrument to position a Hagglunds (a tracked over-snow vehicle) at the southern end of one of the transects within an area. When the vehicle was in position, two 4-wheeled motorbikes (quads) were driven directly east and west from the Hagglunds for 750 m, the drivers registering that longitude as the edge of the transect. Each quad was fitted with a heated box mounted on the handlebars that held a Garmin 12XL GPS, powered from the quad. The Hagglunds was then driven directly North (0° by the compass) over the fast ice at a pace equal to the quads. The quads zigzagged over the ice from the edge of the transect to the centre line. A pilot survey had determined that seal breathing holes could be detected up to 500 m away, haul-out sites were visible from the same distance, and seals resting on the ice surface could be seen from over a kilometre away.

The quad GPSs were set to *traclog*, registering the quad's position every 2.5 minutes. Whenever a seal site was encountered, the quad driver marked the position into the GPS as a waypoint and then used VHF radio to relay information about the site to the Hagglunds. The following information was collected:

Latitude/longitude (in decimal degrees)
Ice conditions, eg, tide cracks and rafted ice
Proximity of site to islands/icebergs
Size of hole (large haul-out, small haul-out, head breathing, nose breathing, or no hole found)
Number and sex of seals hauled out on surface
Number and sex of imprints on the ice around holes
Any evidence of other species using the holes

When the Hagglunds reached the northern end of the transect, the quads returned to the centre line, GPSs turned off and the three vehicles travelled to the centre line of the next transect which was surveyed in the same manner but in a N-S (180° by the compass) direction.

3.2.2 Data analysis

Waypoints and track coordinates were downloaded from the GPS using OziExplorer software (© Des and Lorraine Newman), which converted the data to a format that could be imported into MS Excel. Using ArcView post-survey, the transects were overlaid with a grid pattern to subdivide each transect into 1x1.5 km^2 rectangles. The sighting data for each area within each survey period were then expressed as the number of encounter sites and the number of seals per grid segment. Number of seals per grid segment did not include counts of pups, as counting these would provide a confounding inflation of seal numbers at pupping sites. However, it was assumed that one pup equalled one female seal when less adult females than pups were observed at sites with pups. Number of sites and number of seals per transect grid were the dependent variables for analysis, and independent variables were distance to coast, area and survey period. All significance values were set at $p \leq 0.05$.

The two transects in each area were treated as replicates. A probability plot of the distribution of number of encounters and number of seals per grid showed poor conformity to normality that could not be resolved with transformation, therefore non-parametric tests were used. Transects within each area and each survey period were compared for differences in the dependent variables using Kolmogorov-Smirnov tests. Association of haul-out sites and number of seals hauled out on ice with distance to coast was examined by performing Friedman tests to compare the dependent variables along transects whilst holding the possible covariate of area constant (Dalgaard 2002; M. Hindell, personal communication). Differences in the dependent variables between the different areas were examined using Kruskall-Wallis one-way analysis of variance, testing the null hypothesis that the dependent samples come from the same population or from identical populations with respect to averages (Siegel 1956, Sokal and Rohlf 1995). Differences in dependent variables between the three survey periods were analysed with Friedman tests, comparing survey periods for each area separately.

Post-survey, ArcView (Version 3.2, © ESRI Inc. 1992-1999) was used to map the position of sites that had males only, females only or a mix of males and females. Single sex sites meant that seals seen and imprints in the ice seen at the site were distinguished as being of the same sex. It is not known how long imprints of seals remain visible. Given the low densities of seals that were found during the surveys, no statistics were conducted, but a basic description of the group compositions is provided.

3.3 Results

3.3.1 Site description

During the winter of 2000, the fast ice extended >93 km out from the MacRobertson Land coast (AVHRR images obtained from NOAA website http://www.natice.noaa.gov). The sea ice set in April 2000 and started breaking out to the west of Mawson station from October and to the east from November of the same year.

The ice in the area that extended north of Mawson station (see Figure 3.1) was mostly smooth ice blown clear of the snow. Approximately 16-18 km from the coast the ice was characterised by eroded sastrugi (ridges of snow created by wind) of medium height (30-50 cm) and medium rafting (where the ice cracks and the ice pieces ridge up against and on top of each other).

The fast-ice in the Macey area, ~50 km east of Mawson, was mostly smooth, the main feature of the area being the many large (>100 m^2) icebergs grounded on the sea-bed (water depth < 100m, see Figure 3.1). These large icebergs hemmed in smaller non-grounded bergs. Approximately 18-19 km from the coast, the smooth ice became ridged into medium sastrugi.

In the Colbeck area, ~100km west of Mawson, the sea ice was characterised by sastrugi and low-medium rafting and there were 10 icebergs in the transects. The sea ice was covered with a thick layer of snow that was ridged into medium and heavy sastrugi throughout the transect area. Within 1km of the coast the ice was covered with low sastrugi (<10 cm) over smooth ice.

3.3.2 Seal counts

During the three surveys, 349 seals (including pups) were observed amongst 165 sites across all three areas (see Figure 3.2). No seals were sighted at Colbeck or Macey during the first survey, although at Macey there were 8 sites with evidence of seals. Of all the sites encountered during the three survey periods, only two sites were consistently encountered in all three survey periods and both of these occurred in the Macey area. Nineteen of the 46 sites encountered at Macey in September were re-encountered in October. At Mawson, 1 site from July was re-encountered again in October but was not observed in September, and 3 sites from the 10 encountered in September were re-encountered in October. At Colbeck, there were 5 sites encountered in September but none of these were re-encountered in October, however 6 new sites were encountered in October.

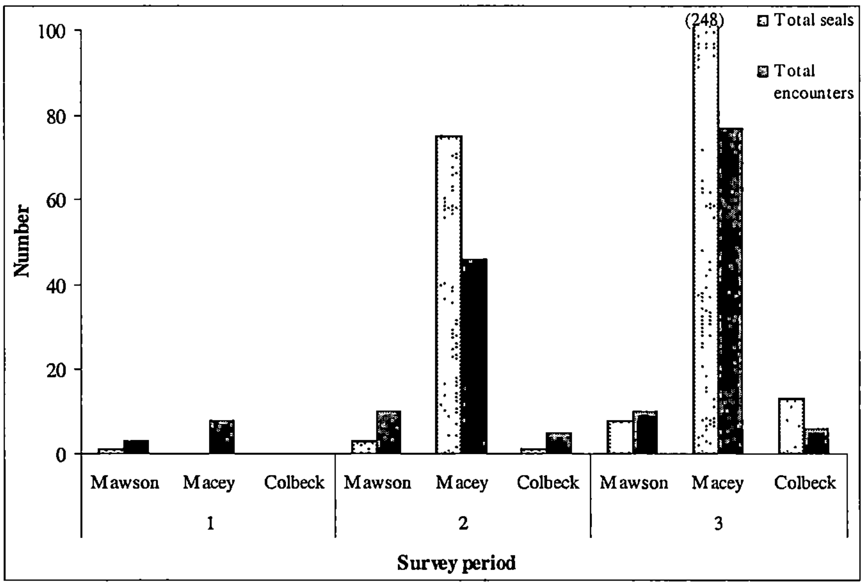


Figure 3.2 Total number of seal sites encountered and number of seals seen at each area during each of the survey periods. The y-axis is cut short so the smaller values are more clearly shown; total number of seals encountered at Macey during survey period 3 is shown in brackets.

3.3.3 Group composition

At Colbeck in Survey 3 (the time when most seals were seen in this area) there were 13 seals sighted and of these 6 were males, 1 was female and 6 were unsexed juveniles (see Figure 3.3). At Mawson in Survey 3, there were 3 males (1 adult and 2 sub-adults) and 5 females (3 adults and 2 sub-adults), and in Survey 2 two unsexed adults plus 1 dead pup were observed. A dead pup was also observed at Macey in Survey 2, along with 27 female and 33 male seals. In Survey 3 at Macey, there were many more females (108) than males (41), and 88 pups were observed as well.

Positions of male only and female only sites had no discernable pattern throughout the transects in all three areas. The number of single sex sites was lower than the number of sites with both sexes present (see Figure 3.4). In the Mawson area, no sites with females only appeared until Survey 3. In the Macey area, the number of sites increased, but the relative proportions of male only, female only and mixed sex sites appeared relatively constant. Pupping sites also occurred throughout the transects in the Macey area. No pupping sites occurred in the transects in the other areas, but in the Colbeck area there were two large (>30 mother-pup pairs) aggregations sighted east of the transects and in the Mawson area a small pupping colony (10 mother-pup pairs) was located approximately 18 km NNW of Mawson station at Sawert Rocks.

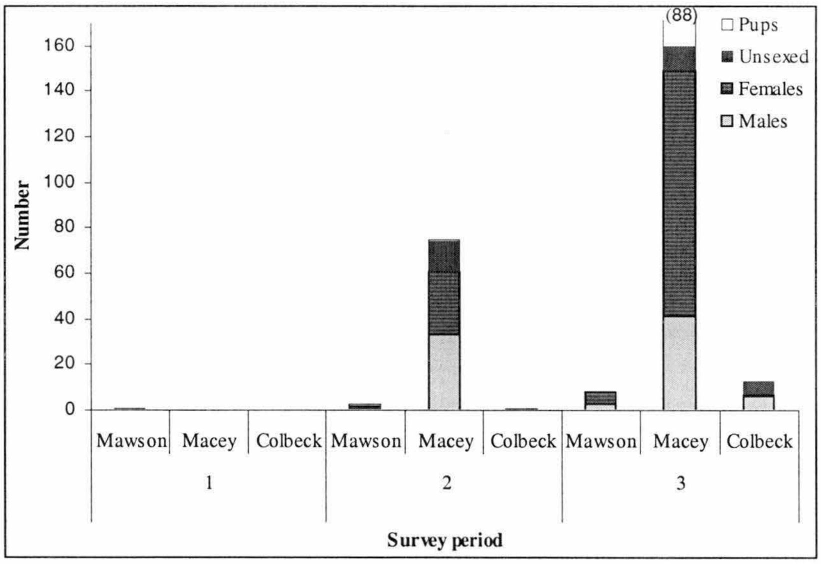


Figure 3.3 Number of males, females, unsexed seals and pups observed at each area within each survey period. The y-axis is cut short so the smaller values are more clearly shown; the number of pups observed at Macey during survey period 3 is shown in brackets.

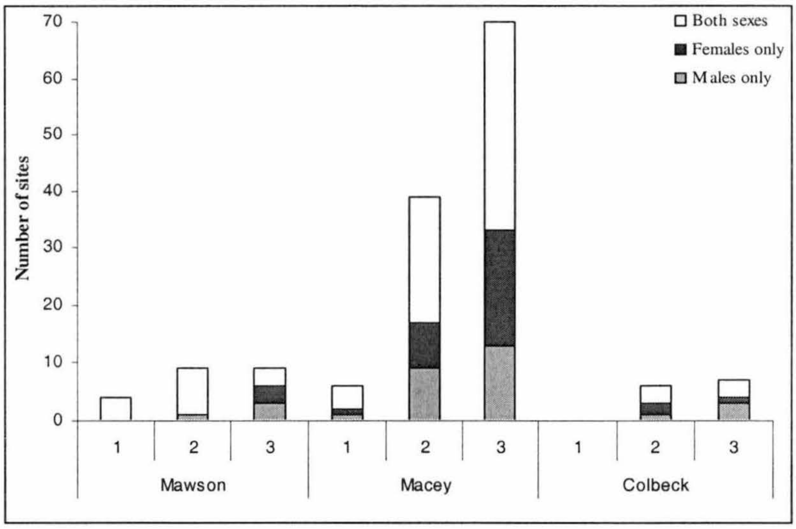


Figure 3.4 Number of sites at each area during each survey period that had evidence of only male and only female Weddell seals (either from imprints or actual seals).

3.3.4 Spatial variation

Kolmogorov-Smirnov tests found no significant difference between transects in any of the areas at the different survey times ($p > 0.10$ for all tests). Thus transect data was combined for subsequent analysis.

No significant variation was found in number of encounters or number of seals between grid segments within areas during each survey period, using Friedman tests (see Table 3.1). Therefore, no association with distance to coast was detected.

Comparing the different areas for number of encounters and number of seals found significant differences between the three areas during each of the survey periods (see Figure 3.5), except that number of seals per area was not significant in Survey 1 (see Table 3.2), due to no seals being seen at Macey or Colbeck. In each survey period, Macey had the greatest number of encounters and Colbeck had the least (see Figure 3.5).

Table 3.1 Results of Friedman tests comparing grids within transects within each area during each survey period.

Survey period	Area	Number of encounters	Number of seals
	Mawson	$H_{19,40} = 17.92$, $p = 0.53$	$H_{19,40} = 19.00$, $p = 0.46$
1	Macey	$H_{19,40} = 16.08$, $p = 0.65$	-
	Colbeck	-	-
	Mawson	$H_{19,40} = 14.67$, $p = 0.74$	$H_{19,40} = 18.47$, $p = 0.49$
2	Macey	$H_{19,40} = 24.10$, $p = 0.19$	$H_{19,40} = 21.81$, $p = 0.29$
	Colbeck	$H_{19,40} = 17.34$, $p = 0.57$	$H_{19,40} = 19.00$, $p = 0.46$
	Mawson	$H_{19,40} = 20.12$, $p = 0.39$	$H_{19,40} = 16.73$, $p = 0.61$
3	Macey	$H_{19,40} = 25.05$, $p = 0.16$	$H_{19,40} = 18.41$, $p = 0.50$
	Colbeck	$H_{19,40} = 21.77$, $p = 0.30$	$H_{19,40} = 16.73$, $p = 0.61$

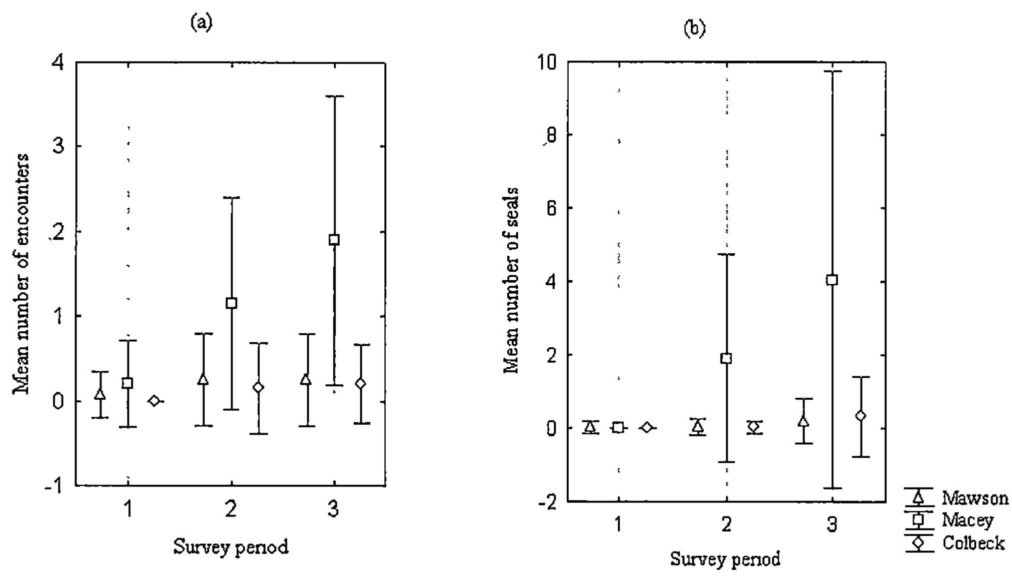


Figure 3.5 Mean number of encounters (a) and mean number of seals (b) ±1 SD per grid segment in each area during each survey period.

Table 3.2 Results of Kruskall-Wallis tests comparing areas within each survey period

Survey period	Number of encounters	Number of seals
1	$H_{2,120} = 6.53$, $p= 0.04$	$H_{2,120} = 2.00$, $p = 0.37$
2	$H_{2,120} = 32.36$, $p<0.01$	$H_{2,120} = 40.72$, $p<0.01$
3	$H_{2,120} = 68.47$, $p<0.01$	$H_{2,120} = 64.30$, $p<0.01$

3.3.5 Temporal variation

Given the significant spatial variation, each area was investigated separately for differences in number of encounters and number of seals (excluding pups) between the three survey periods. Friedman tests found no significant differences between the survey periods for each of the dependent variables (see Table 3.3 and Figure 3.5).

Table 3.3 Results of Friedman tests comparing survey periods within each area.

Area	Number of encounters	Number of seals
Mawson	$X^2 = 3.00$, $p = 0.08$	$X^2 = 3.00$, $p = 0.08$
Macey	$X^2 = 0.33$, $p = 0.56$	$X^2 = 2.00$, $p = 0.16$
Colbeck	$X^2 = 1.00$, $p = 0.32$	$X^2 = 0.00$, $p = 1.00$

3.3.6 Other species

Only Weddell seals were sighted during survey 1. There were four other species sighted during surveys 2 and 3 - crabeater seals *Lobodon carcinophagus*, emperor penguins *Aptenodytes forsteri*, south polar skuas *Catharacta maccormicki* and Adelie penguins *Pygoscelis adeliae*. Crabeater seals were sighted at Macey during Survey 2 (1 unsexed adult at one site) and again in Survey 3 (2 adults, 1 male and 1 female, at 2 sites). Emperor penguins were sighted at Colbeck in Surveys 2 and 3 (at 2 and 5 sites respectively), and at Macey during Surveys 2 and 3 (at 14 and 9 sites respectively). Skuas were sighted at 3 sites in the Macey area during Survey 3. Adelie penguins were sighted during the survey of the transects in the Mawson and Macey areas during Survey 3, but were not associated with any Weddell seal sites.

3.4 Discussion

This study represents the first survey of Weddell seals along the MacRobertson Land coast. It gives preliminary results that will contribute to understanding how the haul-out site occurrence of Weddell seals distribution is linked to environmental variation, particularly in the fast-ice circling Antarctica.

3.4.1 Seal counts and group composition

There were very few Weddell seal haul-out sites that were open in all three of the surveys, but more (30% at Mawson and 41% at Macey) were open in both the September and October surveys. The implications of this are unclear, as there are not enough data to be able to correlate long-term use of sites with particular environmental factors such as bathymetry and ice characteristics. It does indicate however, that the fast ice in this region is a dynamic environment, and that seals make opportunistic use of tide cracks or areas of thinner ice rather than expend energy continually maintaining a hole in the one location.

Prior to these surveys, it was suspected that there may be some spatial separation of sexes and/or ages of seals, especially in the breeding season. Differences in haul-out between sexes between winter and summer may indicate that seals utilise different foraging areas, or it may be due to some sort of social hierarchy. Patterns like this were not detected in the population in the Macey area, but low density of seals may have made it difficult to determine such patterns. There were sites encountered where the seals seen on the surface and seal imprints were either all male or all female, however this does not mean that there were not seals of the other sex using that hole, just that they had not hauled out at that time.

3.4.2 Spatial and temporal variation

There were consistently more seal sites encountered in the Macey area in each of the survey periods. During the second and third survey periods, Macey also had the most seals sighted, with 75 seals at 46 sites in September and 248 seals at 77 sites (not including pups) in October. The density of seal sites is likely to be affected by environmental factors, such as bathymetry and number of icebergs (Lake et al. 2005b). Seals use tide-cracks that form in association with land and icebergs where the ice fractures because the land or grounded iceberg constrains the movement of the ice (Lake et al 2005b). At Macey there is a submarine shelf (Storegg Bank) where the waters are <100m deep (see Figure 3.1), and many of the icebergs in the area are large enough to be grounded. In the other areas, the waters tend to be much deeper, varying from 250-

1000m deep at Colbeck and <100-1000m deep at Mawson (the Mawson transects were over a submarine trough extending into the coastline from the north), and there are less icebergs, possibly because the water is too deep for icebergs to become grounded. There are more seals in the Macey area than in the other areas due to the increased propensity for the sea ice to crack and allow for more haul-out sites to be created and/or maintained.

The different areas showed no differences temporally in the number of encounters or the number of seals. This can be attributed to a lack of power within the non-parametric tests, for the data was not able to be transformed therefore more powerful generalised linear modelling could not be performed. It was expected that number of sites and number of seals would increase over time, for several reasons: 1) seals aggregating in the area as the breeding season approaches (Siniff et al 1977, Kooyman 1981); 2) variation in environmental factors such as light levels, ice thickness and ocean currents, contributing to the seals' ability to create/maintain holes, and 3) warmer temperatures and increased radiation in summer making surface conditions more preferable for haul-out (Lake 1997).

3.4.3 Other species

Other species appear to benefit from the Weddell seals' ability to keep ice holes open. The patterns in sightings of different species at different times and different areas can be associated with the location of breeding sites and timing of breeding seasons, and illustrates the shared influence of sea ice on the air-breathing animals occurring in the fast-ice zone. The presence of penguins at Weddell seal sites is explained by the breeding colonies of Emperor penguins in the Macey and Colbeck areas and Adelie penguins at many islands along the MacRobertson Land coast. Emperor penguins breed during the winter, and were in the Macey and Colbeck areas during all three surveys. However, no birds were sighted in Survey 1 because there is limited movement by birds over the fast-ice at that time of year, as it coincided with the time that females are brooding their newly-hatched young and the males have departed to feed after a long fast (Robertson 1995). More Emperor penguins were seen during subsequent surveys as there is more movement in and out of colonies as the males and females swap chick care and foraging

(Robertson 1995). It appears that Emperor penguins make use of Weddell seal holes, either as breathing holes en-route to offshore foraging areas, or as entry points for foraging under the fast ice.

Adelie penguins spend the winter foraging amongst the pack-ice over the continental shelf break (Kerry et al. 1995, Davis et al. 1996, Clarke et al. 2003). They return to their island-based breeding colonies in mid-October, earlier at lower latitudes (personal observation). Therefore they were not seen during the first two surveys and during the survey of the Colbeck area during period 3 because they had not yet arrived (the Colbeck area was surveyed just prior to the arrival time of the Adelie penguins in that year, officially noted as October 18; personal observation and unpublished CEMP data, Australian Antarctic Division). Adelie penguins were only ever sighted walking over the ice, ignoring possible access points to the water including tide cracks and seal holes.

Crabeater seals have been recorded in winter as preferring to haul-out in regions of dense pack-ice with open leads in areas of high productivity such as near polynyas (McMahon et al. 2002, Burns et al. 2004). As well as being sighted within the transects during surveys 2 and 3, crabeater seals were also regularly sighted at other haul-out sites in the Macey area from late August, usually in conjunction with Weddell seals and emperor penguins. It was not known whether they were foraging under the fast-ice or travelling to other areas with more open water. It seems unlikely that they would be foraging under the ice for krill, their primary food, as krill rarely occurs under ice >50 cm thick (Hempel 1991). This is the first report of crabeater seals occurring in fast-ice areas during winter.

Skuas arrive in early summer as pupping begins (personal observation) and were observed in association with Weddell seal pupping sites, scavenging on discarded placentae and dead pups (Stirling 1977). As Weddell seals were the only air-breathing species observed on the ice surface during Survey 1, I conclude they were the only top-level predator diving under the ice around this time.

3.4.4 Conclusion

This study supports the hypothesis that Weddell seal haul-out sites are associated with factors that contribute to cracking the fast ice and therefore enabling access for the seals (Lake et al. 2005b). However, the results did not determine the point at which there is sufficient distance from land for fast-ice to move freely, and nor was the relationship with distance to ice edge tested for comparison with Lake et al.'s (2005b) findings. Future studies will need to incorporate environmental data collected independently but in conjunction with surveys of Weddell seal haul-out sites. Variables that could be measured are light levels, ice thickness, water depth and oceanography parameters such as current flow beneath the ice. Satellite images can also give information such as distance to coast, ice edge, islands and icebergs that can be used to determine the nature of the association between haul-out site occurrence and tendency for ice to crack. These characteristics can then be used to model the predicted distribution of seals in more in areas of the Antarctic that are inaccessible for surveying. Ground/ice surveys are limited by logistical constraints such as carrying enough fuel for vehicles and safety considerations, but are also useful in that a finer level of detail can be recorded than in an aerial survey.

Whilst this study provides only preliminary results regarding the relationship between Weddell seals and their fast-ice environment, it confirms that haul-out sites are not randomly distributed at the local scale, with differences between different areas along the coast, and that the number of sites and number of seals increases from winter into the breeding season. Longer-term studies of Weddell seal distributions are required in order to determine influence of interannual variations in parameters such as fast-ice extent and ice thickness on the population.

Section of a pupping group in the Macey area, October 2000

Chapter 4: General Discussion

As coastal animals that inhabit the fast-ice and feed over the continental shelf at locations all around Antarctica, Weddell seals experience considerable local variation in fast-ice characteristics and sea-floor topography. For example, water depths around the Vestfold Hills and offshore islands are much shallower than around Mawson, where deep submarine canyons allow penetration of most of the shelf water column to the coastline (Smith and Tréguer 1994, Heil et al. 1996). Differences in bathymetry influence movements of water-masses such as circumpolar deep water and bottom water (Heil et al. 1996), which in turn affects the productivity of the waters (Hempel 1985), ice formation (Heil et al. 1996) and the location of pressure points where ice fractures. Fractured ice lets in light that influences the productivity of the waters underlying the fast-ice sheet (Eicken 1992); whilst water currents and salinities vary with depth which influences the faunal structure.

Given the extent of the fast-ice at Mawson and assuming that most adult seals stay within 50-100 km of their summer breeding colonies throughout the year (Testa 1994, Lake et al. 2005a), we can presume that many of the seals in the Mawson area will be almost exclusively foraging under fast-ice during the winter and not foraging under both fast-ice and heavy pack-ice as they do at McMurdo Sound (Testa 1994) or off the Vestfold Hills (Lake et al. 2005a). This means that the Mawson population of Weddell seals experience environmental conditions very different from seals in other locations around Antarctica, especially in terms of light penetrating the waters. At Mawson, the seals would be foraging in severely restricted light conditions until the fast-ice melts in January (Eicken 1992).

4.1 Variation in diet of Weddell seals at Mawson

In general terms, the range of prey species found in the diet of Weddell seals at Mawson was more diverse than for other populations previously studied (eg, see Lake et al. 2003). Squid (*P. glacialis*) were particularly abundant in early summer but less so in winter. Although the biology of *P. glacialis* is not well documented, individuals are thought to undergo ontogenetic downward migration (Jackson and Lu 1994). Despite the relatively low %FOO of squid in scats, a significant relationship between size of squid and water depth was found, with larger individuals coming from deeper waters near the bottom and smaller individuals coming from shallower waters, showing that Weddell seals may feed upon individuals at different life stages at their corresponding depths.

Interannual variation was detected in Weddell seal diet, primarily in terms of gammarid abundance. Lower abundance of gammarids in seal scats coincided with low krill abundance in the diet of Adelie penguins, which was purported to contribute to poor breeding success of Adelie penguins for that season. Although the direct processes are beyond the scope of this study, it is known that sea ice cover profoundly influences krill (through trapping of larvae within the ice lattice and also because krill feed on sea-ice algae; Hempel 1991) and the benthos (habitat of gammarids) through fallout of organic sediment (Eicken 1992). It is possible that scats of Weddell seals can be used as an indicator of changes in lower-order trophic levels; but that the seals themselves have a broad enough diet to be buffered against changes in one prey type.

The diet of Weddell seals at Mawson shows some differences to other locations. At McMurdo Sound, *Pleuragramma antarcticum* dominates the marine fauna and this is reflected in the diet of seals (Dearborn 1965, Castellini 1992). In the shallow waters of the Vestfold Hills, Weddell seal diet features higher abundances of prawns (Green and Burton 1987, Lake et al. 2003). At Mawson, the diversity of prey species in the diet is attributed to the variety of depths available to the seals in which to forage, from submarine canyons >300 m deep to banks creating shallow waters <100 m. Very little research has been done into determining the influence of the physical environment on availability of resources to seals and how this changes around the continent. This is an important step to fully understanding the niche of Weddell seals in the ecosystem and how they survive in the fast-ice regions throughout the winter.

4.2 Variation in occurrence of haul-out sites along the Mawson coast

Density of Weddell seal haul-out sites was non-randomly distributed at the regional scale on the Mawson coast. This pattern is possibly associated with differences in ice characteristics, affected by bathymetry (and therefore number of icebergs), which influences fracturing of the fast-ice and thus enables access for seals. Lake et al (2005b) determined that distance to coast was an important determining factor for haul-out sites of Weddell seals in the Vestfold Hills; however, in the Mawson area this factor was not an important determinant of density of haul-out sites. Mawson fast-ice is more stable and does not break out easily because it is held in place by offshore islands along the coast.

Several factors were identified as possible determinants of haul-out site locations and density, such as bathymetry, density of icebergs, fast-ice extent, ice thickness and number of tide-cracks. To really understand the relationship between seal-haul out sites and the physical environment, future surveys should incorporate independent assessment of these factors whilst at the same time quantifying the distribution of seal sites. The aim for any future work could be the development of models for predicting distribution of Weddell seals in areas where ground or air surveys are logistically unfeasible, and ultimately work towards a systematic determination of population size.

4.3 Conclusion

This study of Weddell seals has shown that a key environmental feature influencing both the diet and haul-out distribution of Weddell seals is sea-floor topography. This affects the direction of water movements and creates pressure points where ice fractures, enabling Weddell seals' access to air and to the ice surface for resting and pupping. The diversity of prey species in the diet of Weddell seals is a reflection of the variety of habitats at different depths available to the seals for foraging.

The Mawson site is very different to other sites where Weddell seal research has been concentrated, and this thesis has highlighted the need to conduct research at different sites where Weddell seals occur, especially those with unique bathymetric or ice characteristics. I have shown that generalisation of Weddell seal ecological processes, such as trophic interactions, cannot be made from single sites.

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